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## A New Genus and Five New Species of Neotropical Tryphoninae (Hymenoptera: Ichneumonidae)

ANDREW M. R. BENNETT

Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park,  
Toronto, Ontario, Canada, M5S 2C6 [current address: Agriculture and Agri-Food Canada,  
K.W. Neatby Building, 960 Carling Avenue, Ottawa, Ontario Canada, K1A 0C6];  
email: bennetta@agr.gc.ca

**Abstract.**—A new genus of tryphonine ichneumonid, *Boethella* Bennett, n. gen. is described from the Neotropics. Synapomorphies are provided which support the sister group relationship of *Boethella* and *Boethus* Foerster (Tryphonini) (the latter known from the Holarctic, Neotropical and Ethiopian regions). *Boethella darlingi* Bennett, n. sp. is described from eastern Brazil, *B. canilae* Bennett, n. sp. (type species) is described from southern Mexico to eastern Brazil, *B. hubleyi* Bennett, n. sp. is described from southeastern Brazil, *B. guidottiae* Bennett, n. sp. is described from western and central Brazil and *B. curriei* Bennett, n. sp. is described from Peru.

The latest survey of the family Ichneumonidae (Yu and Horstmann 1997) listed 21,805 described extant species classified into 1485 genera. These genera are assigned to 36 or 37 extant subfamilies depending on opinion (Wahl 1990, Yu and Horstmann 1997, Gauld 2000, Gauld and Wahl 2000). Some studies have attempted to elucidate the subfamily relationships (Wahl 1991, Wahl and Gauld 1998, Quicke *et al.* 2000); however, to date, no complete subfamily phylogeny is available for the Ichneumonidae. A recent study of one subfamily, the Tryphoninae, was undertaken in order to ascertain its placement within the family (Bennett 2002). In the process of this study, two new genera were discovered, one of which is described below. The other new genus from the tribe Oedemopsini will be described elsewhere allowing a full discussion of the characters and relationships of the 12 extant oedemopsine genera.

The subfamily Tryphoninae comprises 1170 described species (Yu and Horstmann 1997) assigned to 53 described genera in seven tribes (Bennett 2002). The subfamily is cosmopolitan with its centre of

diversity in the Holarctic Region (Kasparyan 1973). Tryphonines are koinobiont ectoparasitoids of lepidopterans and sawflies of the families Xyelidae, Tenthredinidae, Cimbicidae, Diprionidae and Argidae. They exhibit the uniquely derived trait of bearing eggs that travel down the outside of the ovipositor (Kasparyan 1973) (although this trait is unknown in the Idiogrammatini). The apical end of the stalk (which bears an anchor in most genera) travels down the inside of the ovipositor so that the body of the egg is suspended by the stalk ventral to the ovipositor. This anchor is pushed through the host integument during oviposition, thereby holding the egg in place until hatching. Females of most genera of tryphonines have the habit of bearing an egg on their ovipositor while searching for their hosts (Kasparyan 1973) which provides an incontrovertible character to identify them as tryphonines. Male tryphonines and females that do not carry eggs externally during host searching (e.g. the Phytodietini) are more difficult to recognize because the subfamily is relatively heterogeneous in structure with some taxa re-

sembling ctenopelmatines, whereas others resemble phygadeuontine cryptines, banchines or ophionines.

During studies at the American Entomological Institute (AEIC), I found a series of Neotropical specimens set aside by Henry Townes labeled "New Genus near *Boethus*". Two of these putative new species were included in a cladistic analysis of tryphonine generic relationships (Bennett 2002) to examine their status and their hypothesized relatedness to *Boethus*. The cladistic analysis verified the generic status of this new genus as well as its sister group relationship with *Boethus* (see Bennett 2002, Bennett in prep. and below). The present paper describes this new taxon as *Boethella* Bennett, n. gen., the 54th genus of the Tryphoninae (37th genus of the tribe Tryphonini).

## MATERIALS AND METHODS

Specimens were borrowed from and are deposited in the American Entomological Institute, Gainesville, FL, USA (AEIC) (D. Wahl) and the Canadian National Collection, Ottawa, Canada (CNC) (J. Huber). Examination of other major ichneumonid collections (e.g. INBio Costa Rica and The Natural History Museum, London) did not reveal more specimens of this genus.

Morphological terms follow Townes (1969) with some modifications: supra-antennal area for 'frons', supraclypeal area for 'face', malar space for 'cheek', epicnemial carina for 'prepectal carina' and laterotergites for 'epipleura'. MS1, MS2 refers to metasomal segments 1, 2 etc. T1 etc. refers to the tergites of metasomal segments 1 etc. and S1 etc. refers to the sternites of metasomal segment 1, etc. Wing venation terms follow the Comstock-Needham system as updated by Ross (1936) and incorporates the recommendations of Goulet and Huber (1993) except for naming of the vein that forms the distal edge of fore wing cell 1+2Rs (the 'areolet' of Townes 1969) which is referred to

as vein 3rs-m in accordance with Gauld (1997).

## TAXONOMIC PLACEMENT

The strongest evidence that a taxon belongs to the Tryphoninae is that its females bear stalked eggs that travel down the outside of the ovipositor. The egg of *Boethella* is not known, therefore the placement of *Boethella* in the Tryphoninae is not certain. Most adult tryphonines exhibit the following characters: clypeus with an apical fringe of hairs; cell 1 + 2Rs (areolet) of fore wing triangular to subrectangular; spiracle of T1 anterior to middle; T1 with a glymma present; dorsal valve of ovipositor high (not strongly tapered) and unnotched subapically. Of these characters, *Boethella* possesses the clypeal fringe of hairs (albeit sparse) and the high, unnotched ovipositor (Fig. 7). The latter character precludes the placement of *Boethella* in the Ctenopelmatinae. In addition, the areolet of the fore wing of *Boethella* (Fig. 1) resembles other tryphonines which have an open areolet (i.e., if the areolet were closed, it would be triangular, not pentagonal as in cryptines or ichneumonines or rhombic as in mesochorines). On the basis of these three characters, *Boethella* fits best in the subfamily Tryphoninae (compared to all other extant subfamilies), despite its apomorphic structure of T1 (i.e., glymma absent and spiracle positioned posteriorly which is the condition found in cryptines and ichneumonines). It should be noted that *Boethella* is not the only genus of tryphonine with the latter two character states (e.g., *Sphinctus* Gravener and *Ankylophon* Gauld).

*Boethella* can further be assigned to the tribe Tryphonini because of its apomorphic pectinate tarsal claws that within the Tryphoninae are known only in the tribes Tryphonini, Exenterini (= the *Exenterus* group of genera, see Bennett 2002), Sphinctini and Phytodietini. *Boethella* does not possess any apomorphies that would place it in either of the latter two tribes

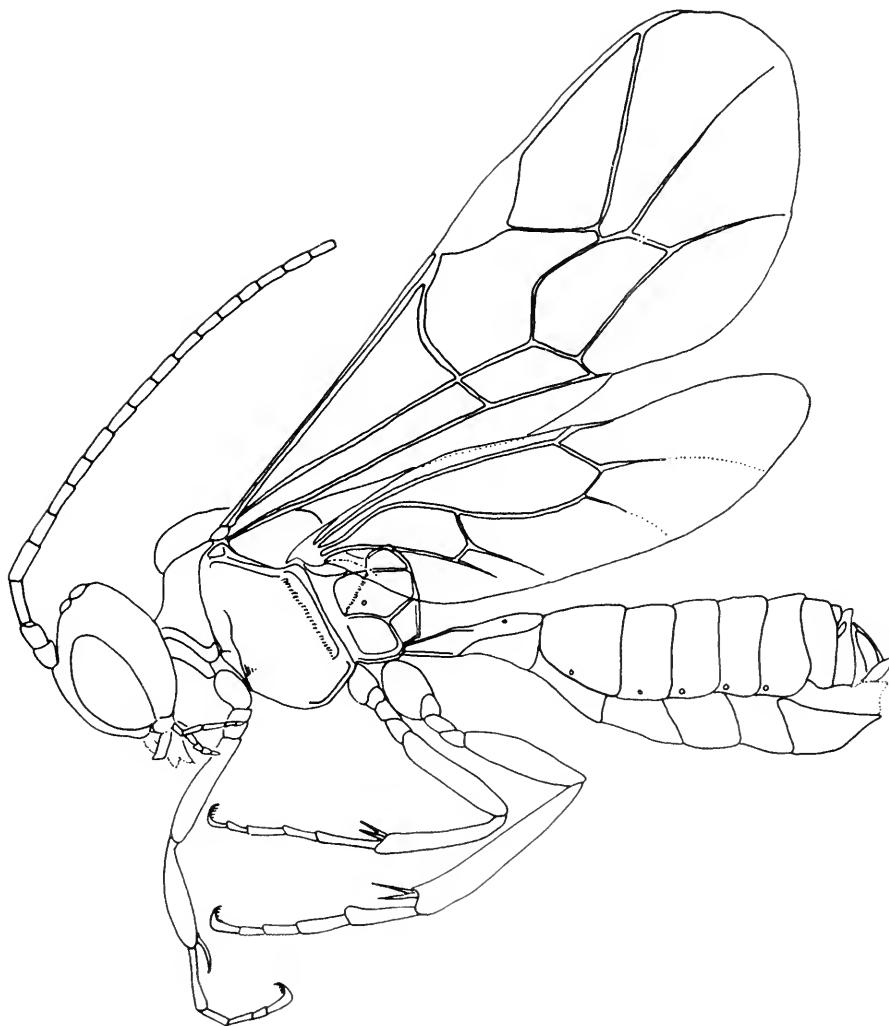


Fig. 1. *Boethella canilac*, holotype female, habitus.

(e.g., the strongly pointed apical edge of the clypeus in the Sphinctini or the loss of propodeal carinae in the Phytodietini). *Boethella* also cannot be assigned to the Ex-exterini because it has paired tibial spurs on both the middle and hind legs (the Ex-exterini have the autapomorphies of only one spur on the middle leg and no spurs on the hind leg).

The sister group relationship of *Boethella* and *Boethus* is supported by the following synapomorphies: occipital carina absent; synomia absent; notauli absent; fore wing

vein 2m-cu with one bulla; fore wing vein 3rs-m absent (areolet open); T1 petiolate; spiracle of T1 in posterior 0.4. A complete cladistic analysis describing character polarities and the relationships of all tryphonine genera including *Boethus* and *Boethella* is given in Bennett (2002) and Bennett (in prep.). *Boethella* can be distinguished from *Boethus* by the former's possession of propodeal, epicnemial and submetapleural carinae (all of which are absent in *Boethus*). In addition, the glymma is absent in *Boethella* (present in *Boe-*

thus). *Boethella* is exclusively Neotropical and the majority of species of *Boethus* are known from the Neotropical and southern Nearctic regions (Townes *et al.* 1992); however, several Ethiopian species of *Boethus* are known (Scaramozzino 1991) as well as one Palaearctic species (Kasparyan 1973).

***Boethella* Bennett, n. gen.**

*Type species*.—*Boethella caulac* Bennett, by original designation.

*Diagnosis*.—Distinguished from other genera of tryphonines by the combination of: 1) occipital carina absent; 2) propodeal carinae present (Fig. 6). In addition, the ovipositor of *Boethella* is distinctive within the Tryphoninae (slightly upcurved with a high, wide, apically rounded dorsal valve that strongly overlaps the ventral valve medially) (Fig. 7).

*Description*.—Fore wing length 2.9 to 4.8 mm; clypeus slightly rounded in profile, without a transverse line separating it into dorsal and ventral faces, apical margin truncate to slightly rounded in anterior view, strongly impressed laterally (Figs. 2 and 3) without medial paired tubercles (medial notch absent), clypeal fringe of hairs present, but sparse; malar space obliterated (mandibular socket contiguous with ventral edge of eye) (Fig. 2) except in *B. darliugi* space is 0.5 times basal width of mandible (Fig. 3); lower mandibular condyles separated by distance greater than distance of inner eye margins at level of clypeal foveae; mandible with teeth subequal in width and height, moderately convex in cross-section near base; labiomaxillary complex moderately elongate, glossae visible in anterior view in most specimens (Fig. 1); occipital carina absent; postgena without a tooth; supra-antennal area without a horn or carina; antennal sockets separated by distance greater than 0.5 diameter of socket; eyes without prominent setae; epomia absent (Fig. 1); dorso-posterior region of pronotum not strongly thickened in dorsal view; epicnemial carina present, not dorsally curving toward

anterior edge of mesopleuron (Figs. 1, 4–5); auxiliary carina of mesopleuron either long and joining epicnemial carina (Figs. 4–5) or short and not joining (Fig. 1); sternaulus present (Figs. 1, 4–5); subtegular ridge slightly curving out laterally, not produced into a vertical lamella that nearly reaches tegula when tegula is down; notauli absent; projection on posterolateral edge of mesoscutum absent; carinae of scutellum present at base only; propodeal carinae all present except lateral longitudinal carinae absent (Fig. 6), medial longitudinal carinae strongly raised, medial portion of posterior transverse carina weak; submetapleural carina present; fore tibia without an anterior, apical tooth; fore tibial spur evenly curved; middle and hind trochanters two segmented; middle and hind tibiae each with two spurs; tarsal claws pectinate to apex or nearly to apex (Fig. 1); fore wing vein 3rs-m absent (Fig. 1); fore wing vein 2m-cu weakly to strongly inclivous with one bulla (Fig. 1); wings hyaline to moderately infumate; T1 petiolate (Fig. 6) with spiracle at 0.6 to 0.75, dorsal longitudinal carinae absent (Fig. 6), dorsolateral longitudinal carinae present but not extending to spiracle (Fig. 1); glymma of T1 absent (Fig. 1) (slight depression present ventral to dorsolateral longitudinal carina in some specimens, but not a glymma); T1 and T2 not fused, their sculpture impunctate; S1 not fused to T1, membranous portion of S1 not or only slightly projecting lateral to sclerotized portion of T1; T2 without a transverse postmedian groove or oblique grooves delineating the anterolateral corners; laterotergites of MS2 to MS4 separated from tergites by a complete crease; T6 to T8 not strongly turned anteriorly under T5; ovipositor (only known in two species) shorter than apical depth of metasoma, moderately upcurved, dorsal valve thick and rounded apically, overlapping ventral valve laterally (Fig. 7).

*Mature larva*.—Unknown.

*Egg*.—Unknown.

**Hosts.**—Unknown. The sister genus *Boethus* has been reared from argid sawflies (Townes *et al.* 1992, Gauld 1997).

**Distribution.**—Southern Mexico, Peru and Brazil.

**Species included.**—Five species (see key and descriptions below).

**Etymology.**—*Boethella* is a modification of *Boethus* (which means “helper” in Greek) indicating its close relationship with this genus. Its gender is feminine.

#### KEY TO THE SPECIES OF *BOETHELLA* BENNETT

- 1 Malar space 0.5 times basal width of mandible (Fig. 3) (eastern Brazil) ..... *darlingi* Bennett, n. sp.
- Malar space obliterated; dorsal edge of socket of mandible contiguous with ventral edge of eye (Fig. 2) ..... 2
- 2(1) Mesopleuron with auxiliary carina short, not extending to epicnemial carina (Fig. 1) ..... 3
- Mesopleuron with auxiliary carina extending from anterior edge and joining epicnemial carina slightly ventral to ventral edge of pronotum (Figs. 4 and 5) ..... 4
- 3(2) Hind tibia brown. (Brazil to southern Mexico) ..... *canilae* Bennett, n. sp.
- Hind tibia with basal 0.7 yellow, apical 0.3 brown (Brazil—Santa Catarina) ..... *hubleyi* Bennett, n. sp.
- 4(2) Epicnemial carina extending dorsal to point of union of auxiliary carina by at least the length of auxiliary carina (Fig. 4). T4 predominantly brown, yellow laterally and with a yellow medial longitudinal stripe or spot in some specimens (Peru) ..... *curriei* Bennett, n. sp.
- Epicnemial carina extending dorsal to point of union of the auxiliary carina by much less than the length of auxiliary carina (Fig. 5), or not extending at all. T4 entirely yellow or yellow with a trace of brown in apical 0.2 and with a longitudinal brown or brown and white region in medial 0.3 (Brazil: Mato Grosso and Amazonas) ..... *guidottiae* Bennett, n. sp.

#### *Boethella darlingi* Bennett, n. sp.

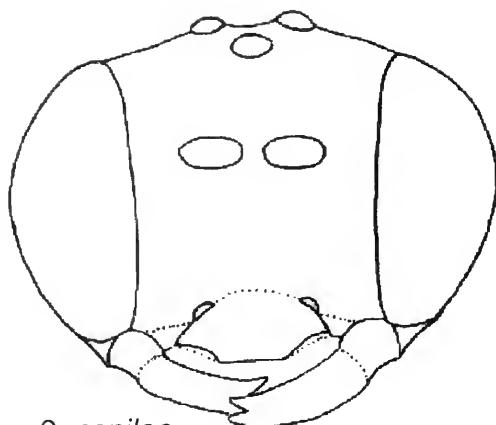
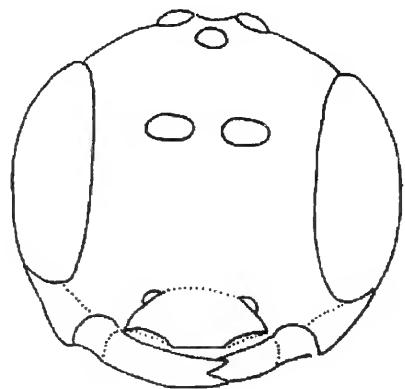
Fig. 3

**Diagnosis.**—Distinguished from other species of *Boethella* by having the malar space 0.5 times basal width of mandible (Fig. 3) (not zero times basal width).

**Female.**—Unknown.

**Male (holotype).**—Fore wing length 3.5 mm; medial part of apical edge of clypeus slightly convex in anterior view, without emargination; groove between clypeus and supraclypeal area weak laterally so that base of clypeus is relatively flat; malar space 0.5 times basal width of mandible; antenna with fourteen flagellomeres; auxiliary carina of mesopleuron short, not joining epicnemial carina; abscissa of fore wing vein M between 3rs-m and 2m-cu

greater than 0.75 length of 2m-cu; spiracle of T1 posterior to 0.7. Orange; antenna except anterior side of apical two to three flagellomeres, apical 0.2 of mandible, posterior of occiput medial to inner margin of eyes, area between ocelli, pronotum along dorsal edge, lateral lobes of mesoscutum and anterior 0.3 of medial lobe, scuto-scutellar groove, ventral edge of scutellum, mesopleuron except dorsoanterior quarter, mesosternum except small region medioposteriorly; dorsal and ventral edges of metapostnotum, anterior groove of propodeum including base of medial longitudinal carinae, ventroanterior corner of metapleuron; apical 0.8 of hind tibia, hind tarsus, wing veins and stigma, T2 except anterior 0.2, lateral 0.2 and posterior 0.2,

2. *canilae*3. *darlingi*

Figs. 2-3. *Boethella* spp. male, anterior view of head. 2, *B. canilae*, paratype. 3, *B. darlingi*, holotype.

T3 to T7 except posterior 0.2 brown; clypeus, ventral 0.6 of supraclypeal area, ventral 0.5 of gena, propleuron, ventral 0.2 of pronotum, fore leg except coxa, entire middle leg, coxa, trochanter, femur and basal 0.2 of tibia of hind leg, T1, anterior 0.2 and lateral 0.2 of T2 yellow; dorsal 0.8 of pronotum except dorsal ridge and medial region of petiolar region of propodeum brownish orange; mouthparts except apical 0.5 of mandible, anterior side of apical two to three flagellomeres, fore coxa and metasomal sternites white; posterior 0.2 of T2 to T6 translucent white; gonoforceps light brown; wings strongly infumate basally, fading to hyaline apically.

*Material*.—Holotype ♂: BRAZIL, Rio de Janeiro State, Guanabara, Rio Grande, Represa, 1-31.iii.1972 (Alvarenga) (AEIC).

*Etymology*.—This species is named in honour of Dr. D. C. Darling, senior curator at the Royal Ontario Museum, in recognition of his long-standing appreciation of the magnificence of the family Ichneumonidae.

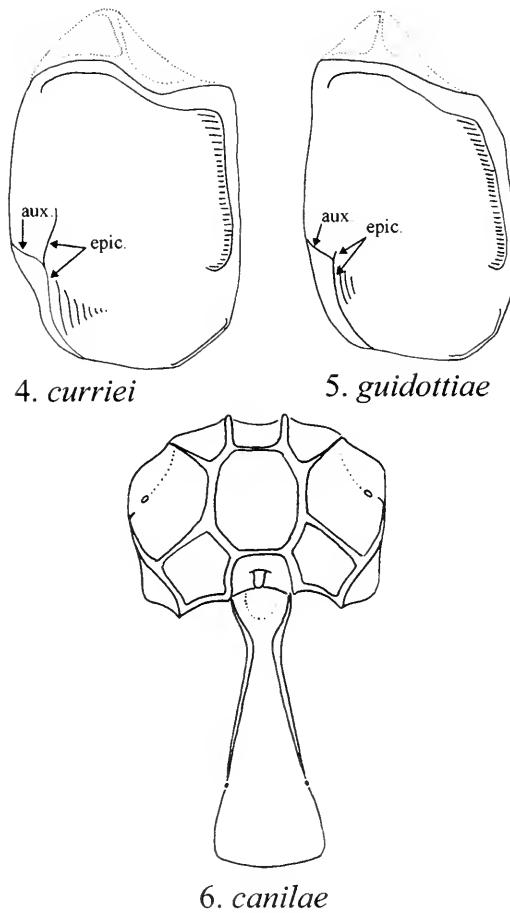
*Comments*.—Known only from the holotype. *Boethella darlingi* may be the sister species of the other four species of *Boethella* because it lacks the obliterated malar space that is synapomorphic of these four species.

*Boethella canilae* Bennett n. sp.

Figs. 1-2, 6-7

*Diagnosis*.—Distinguished from other species of *Boethella* by the combination of all: 1) malar space obliterated (mandibular socket contiguous with ventral edge of eye) (Fig. 2); 2) auxiliary carina of mesopleuron short, not joining epicnemial carina (Fig. 1); 3) hind tibia brown.

*Female (holotype)*.—Fore wing length 4.1 mm; medial part of apical edge of clypeus slightly and broadly emarginate; groove between clypeus and supraclypeal area moderately strong laterally; malar space obliterated (dorsal edge of mandibular socket contiguous with ventral edge of eye) (Fig. 2); antenna with sixteen flagellomeres; auxiliary carina of mesopleuron short, not joining epicnemial carina (Fig. 1); abscissa of fore wing vein M between 3rs-m and 2m-cu less than 0.5 length of 2m-cu; spiracle of T1 anterior to 0.7. Yellowish orange; apical 0.2 of mandible, antenna except apical flagellomere, occiput posterolaterally, posteriorly and in a longitudinal stripe extending posteriorly from between lateral ocelli, dorsal 0.8 of pronotum, tegula, anterior 0.5 of medial lobe mesoscutum and all of lateral lobes, ventral 0.7 of mesopleuron except anterior to epicnemial carina and in ventroposterior corner, mesosternum except medial 0.3, metanotum, hind tibia and tarsus,



Figs. 4–6. *Boethella* spp. 4–5, Male, lateral view of mesopleuron: aux. = auxiliary carina, epic. = epicnemial carina. 4. *B. curriei*, paratype. 5. *B. guidottiae*, paratype male. 6. *B. canilae*, holotype female, dorso-posterior view of propodeum and first metasomal segment.

wing veins and stigma, spot occupying posterior 0.5 and lateral 0.3 of T2, T3 to T7 except posterior 0.2 and triangular-shaped medial portions of T4 to T7 brown; head (except antenna, mouthparts and occiput as noted above), ventral 0.2 of pronotum, posterior 0.5 of medial lobe of mesoscutum, scutellum, dorsal 0.3 of mesopleuron, anterior to epicnemial carina and in ventroposterior corner orange; posterior 0.2 of T2, posterior 0.2 and lateral 0.2 of T3 to T7, medial triangular portions of T4 to T7, metasomal epipleura and sterna including

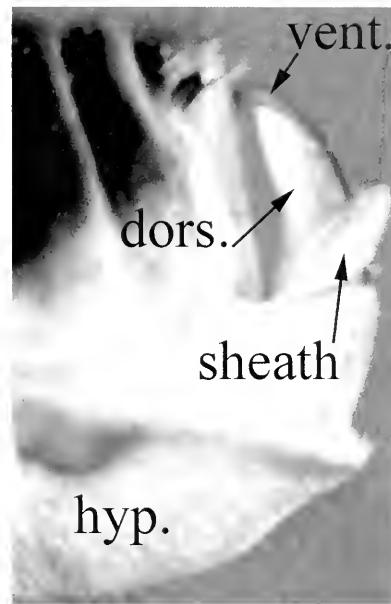


Fig. 7. *Boethella canilae*, holotype female, lateral view of posterior of metasoma showing ovipositor: vent. = ventral valve of ovipositor, dors. = dorsal valve of ovipositor, sheath = ovipositor sheath, hyp = hypopygium.

hypopygium whitish yellow; dorsal valve of ovipositor, ovipositor sheath and membranes at base of ovipositor white; apical flagellomere light brown; membrane of wings hyaline with a trace of infumation apically in fore wing.

*Male*.—Same as female except fore wing length 2.9 to 4.8 mm and antenna with fifteen to eighteen flagellomeres. Colour variations: Dark morph as female, except all flagellomeres brown, occiput with less brown posterolaterally, apical 0.2 of hind tibia brown in some specimens and T2 completely brown except orange in a triangular region basomedially and yellowish white in posterior 0.2; gonoforceps light brown. Light morph as female except clypeus, supraclypeal area and orbits yellowish orange; occiput, pronotum, mesoscutum, scutellum and mesopleuron completely orange; T2 entirely brown except anterolateral corners (or entire anterior 0.1) orange, posterior 0.2 yellowish-white; gonoforceps light brown. Inter morph as

light morph except apical flagellomere only light brown at apex; lateral lobes of mesoscutum completely brown; dorsal 0.5 of pronotum orange brown.

**Material.**—Holotype ♀, BRAZIL, Espírito Santo, Castelo, 1–30.xi.1976 (*M. Alvarenga*) (AEIC). Paratypes. 3 ♂, same data as holotype; 1 ♂, São Paulo State, São José do Barreiro, Serra da Bocaina, 22°37'59"S, 44°34'59"W, 1650 m, 1–30.xi.1969, (*Alvarenga and Seabra*) (AEIC); 1 ♂, MEXICO, Chiapas, 10 km south of Ocozocoautla, 1220 m, 2.viii.1962. (*H. Milliron*) (CNCI).

**Etymology.**—This species is named in honour of Dr. C. Canil in recognition of her exemplary volunteer work at the Royal Ontario Museum.

**Comments.**—*Boethella canilae* is quite variable in colour with the pronotum, mesopleuron and mesoscutum ranging from predominantly brown to completely orange (in same collection site). The male specimen from Mexico is smaller than the other males (fore wing = 2.9 mm) but appears to be conspecific (similar to the light morph males except that T2 and T3 are orange brown instead of brown). The specimen is in relatively poor condition and newer material from Mexico may reveal structural differences that distinguish this population as a distinct species.

#### *Boethella guidottiae* Bennett, n. sp.

Fig. 5

**Diagnosis.**—Distinguished from other species of *Boethella*, by the combination of: 1) auxiliary carina of mesopleuron long, joining epicnemial carina, the latter extending only slightly dorsal to point of union with auxiliary carina or not extending (Fig. 5); 2) T4 predominantly yellow.

**Female (holotype).**—Fore wing length 4.0 mm; medial part of apical edge of clypeus with a slight, narrow emargination; groove between clypeus and supraclypeal area moderately strong laterally; malar space obliterated (dorsal edge of mandibular socket contiguous with ventral edge of eye); antenna with seventeen flagello-

meres; auxiliary carina of mesopleuron long, joining epicnemial carina, the latter extending only slightly dorsal to point of union with auxiliary carina (Fig. 5); abscissa of fore wing vein M between 3rs-m and 2m-cu less than 0.5 length of 2m-cu; spiracle of T1 anterior to 0.7. Yellow; basal 0.5 of mandible, apical five flagellomeres of antenna, medial 0.5 of propleuron, medial 0.2 of mesosternum, entire metapleuron, coxa and trochanter of fore and middle legs, tarsus of fore leg whitish yellow; posterior 0.2 of T2 to T5 as well as lateral edges ventral to spiracle, medial triangular region (widest in posterior) on T3 to T7, metasomal sternites, hypopygium except for a triangular stripe just ventral to dorsal edge, membranes around ovipositor white; scape, pedicel, apical 0.3 of hind tibia, hind tarsus, stigma, apical wing veins and narrow border around medial triangular regions of T3 to T7 yellowish brown; supra-antennal area, vertex, occiput, dorsal 0.3 of gena, dorsal 0.5 of pronotum and mesoscutum yellowish orange; apical 0.2 of mandibles, flagellum except apical five flagellomeres, basal wing veins brown; wing membrane weakly to moderately infumate anteriorly and apically, hyaline posteriorly and subapically.

**Male.**—Similar to female except apical edge of clypeus slightly convex to truncate medially, (emargination present in only some male specimens); fore wing length 3.2 to 4.8 mm; antenna with sixteen to nineteen flagellomeres. Colour variations: Light morph similar to female except apical two to seven flagellomeres whitish yellow and in most specimens, medial 0.5 of T6 and all of T7 yellowish brown; gonoforceps whitish yellow. Dark morph orange; clypeus, mouthparts except apical 0.6 of mandible, ventral 0.5 of pronotum, propleuron, metapleuron, propodeum, fore leg, middle leg, coxa, trochanter and femur of hind leg yellow; apical two to four flagellomeres and sternites of metasoma whitish yellow; all structures that are brown in female are also brown in

dark morph male as are all wing veins and stigma; T2 to T7 vary from yellow to light brown, tending to be more brown medially and posteriorly, apical 0.1 to 0.2 of each tergite may be white or uniform with rest of tergite, some specimens are also similar to holotype with medial 0.3 to 0.5 of T3 to T7 with unpigmented, triangular regions which may indicate incomplete sclerotization of these segments (a longitudinal, medial suture line is also present on the posterior tergites in these specimens); basal 0.7 to 0.8 of hind tibia may be yellow to brownish yellow (but base always lighter than apical 0.2 which is brown); gonoforceps yellowish orange to whitish brown.

*Material.*—Holotype ♀, BRAZIL, Mato Grosso, Sinop, 12°31'S, 55°37'W, Malaise Trap, 1-31.x.1974 (M. Alvarenga) (CNCI). Paratypes. 5 ♂, same data as holotype except one from 1-31.x.1976 and three 1-31.xi.1975; 3 ♂, same data as holotype except 1-31.x.1976 (AEIC); 2 ♂, Amazonas, 4°33'S, 71°38'W, 1-30.ix.1979 (Alvarenga) (AEIC).

*Etymology.*—This species is named in honour of Ms. A. Guidotti in recognition of her dedicated work as technician of the entomology collection of the Royal Ontario Museum.

***Boethella hubleyi* Bennett, n. sp.**

*Diagnosis.*—Distinguished from other species of *Boethella* by the combination of all: 1) malar space obliterated (mandibular socket contiguous with ventral edge of eye); 2) auxiliary carina of mesopleuron short, not joining epicnemial carina; 3) hind tibia yellowish orange in basal 0.7, brown apically.

*Female (holotype).*—Fore wing length 4.5 mm; medial part of apical edge of clypeus slightly and broadly emarginate; groove between clypeus and supraclypeal area moderately strong laterally; malar space obliterated (dorsal edge of mandibular socket contiguous with ventral edge of eye); antenna with seventeen flagello-

meres; auxiliary carina of mesopleuron short, not joining epicnemial carina; abscissa of fore wing vein M between 3rs-m and 2m-cu less than 0.5 length of 2m-cu; spiracle of T1 anterior to 0.7. Yellowish orange; apical 0.2 of mandible, antennae except apical two flagellomeres, anterior 0.5 of medial lobe of mesoscutum, lateral lobe of mesoscutum except anterior, lateral and medial edges, mesopleuron, mesosternum except medial 0.2, apical 0.3 of hind tibia, hind tarsomeres, wing veins, stigma and T3 to T7 except posterior 0.2 and lateral 0.1 to 0.2 brown; occiput medioposteriorly, pronotum, tegula, posterior 0.5 of medial lobe of mesoscutum, anterior, lateral and medial edges of lateral lobes of mesoscutum, scutellum, T2, lateral 0.2 of T3, lateral 0.1 of T4 to T7 orange; palpi, basal 0.8 of mandibles, fore and middle coxa and trochanter and anterior 0.7 of T1 whitish yellow; apical two flagellomeres light brown; membrane of wings hyaline with a trace of infumation apically in fore wing.

*Male.*—Unknown.

*Material.*—Holotype ♀, BRAZIL, Santa Catarina, 27°11'S, 52°23'W, 300-500m, 25.viii.1962 (F. Plaumann) (CNCI).

*Etymology.*—This species is named in honour of Mr. B. Hubley in recognition of his tireless work as collection manager of entomology at the Royal Ontario Museum.

*Comments.*—Known only from the holotype. Colours in fresh material may be more contrasting because of the age and condition of the holotype at time of description. *Boethella hubleyi* is similar to *B. canilae* but the former can be distinguished by the bi-coloured hind tibia. Similar colouration of the hind tibia is only known in *B. guidottiae*, however this can be distinguished from *B. hubleyi* by the structure of the epicnemial carina.

***Boethella curriei* Bennett, n. sp.**

Fig. 4

*Diagnosis.*—Distinguished from other species of *Boethella* by the combination of:

1) the auxiliary carina of mesopleuron long, joining epicnemial carina, the latter extending dorsal to point of union of auxiliary carina by at least the length of auxiliary carina (Fig. 4); 2) T4 predominantly brown.

*Female*.—Unknown.

*Male*.—Fore wing length 3.2 to 3.8 mm; medial part of apical edge of clypeus slightly and broadly emarginate; groove between clypeus and supraclypeal area moderately strong laterally; malar space obliterated (dorsal edge of mandibular socket contiguous with ventral edge of eye); antenna with sixteen flagellomeres; auxiliary carina of mesopleuron long, joining epicnemial carina, the latter extending dorsal to point of union of auxiliary carina by at least the length of auxiliary carina; abscissa of fore wing vein M between 3rs-m and 2m-cu less than 0.5 length of 2m-cu; spiracle of T1 anterior to 0.7. Yellowish orange; apical 0.2 of mandible, antenna except for apical one to two flagellomeres, hind tibia (except in basal 0.2 in some specimens), hind tarsus, wing veins and stigma brown (ventral part of stigma light brown in some specimens); dorsal 0.5 of head, dorsal 0.5 of pronotum and mesoscutum orange (head and pronotum blend uniformly from orange dorsally to yellowish orange ventrally); basal 0.8 of mandibles, palpi, fore and middle legs, propodeum, lateral 0.2 of T2 to T4, posterior 0.1 to 0.2 of T3 to T4 and thin, medial longitudinal stripe on T4 to T7 yellow; tegula, medial 0.6 of T4, (except for posterior 0.1 to 0.2 and medial stripe), medial 0.8 of T5 (except for medial stripe), all of T6 and T7 (except for medial stripe) yellowish brown; apical one to two flagellomeres and gonoforceps whitish brown; sternites of metasoma yellowish white; glossa white; wings strongly infumate basally and dorsally, hyaline subapically and posteriorly and weakly infumate apically. Colour variation: specimen caught 1–15.x.1962 is lighter than other two specimens—structures described above as or-

ange are more yellowish orange and yellowish orange structures more yellow; hind tibia yellow in basal 0.2, yellowish brown medially, brown apically; medial longitudinal stripe on T4 to T7 less prominent; T4 completely yellowish brown except for anterolateral corners and posterior 0.2.

*Material*.—Holotype ♂, PERU, Cusco, near Marcapata, Avispas, 1–30.ix.1962 (L. Peña) (AEIC). Paratypes. 1 ♂, same data as holotype except 1–15.x.1962; 1 ♂, same as holotype except 20–30.ix.1962.

*Etymology*.—This species is named in honour of Dr. D. C. Currie, curator and keeper of black flies at the Royal Ontario Museum, in recognition of his unfathomable appreciation of fried spam sandwiches.

*Comments*.—The specimen caught 1–15.x.1962 is not only lighter in colour than the other two specimens, but also has a much less pronounced sternaulus and a weaker, shorter epicnemial carina. Additional material is necessary to determine if these differences are intra- or interspecific.

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## Foraging Strategy and Pollen Preferences of *Andrena vaga* (Panzer) and *Colletes cunicularius* (L.) (Hymenoptera: Apidae)

INGE BISCHOFF, KERSTIN FELTGEN, AND DORIS BRECKNER

(IB) Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160,  
D-53113 Bonn, Germany, email: i.bischoff.zfmk@uni-bonn.de;

(KF) Dottendorferstr. 29, D-53123 Bonn, Germany, email: kerstin.feltgen@web.de;  
(DB) Johann-Sebastian-Bach-Str. 4, D-77654 Offenbach, Germany

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**Abstract.**—*Andrena vaga* (Panzer) and *Colletes cunicularius* (L.), both vernal ground nesting bees, were studied in the years of 1996–1999 in a lowbush heath near Cologne, western Germany. Both species are solitarily but nest gregariously and sometimes form large aggregations with thousands of nests. They are reported to feed strictly oligoleptic on the genus *Salix*. We observed the daily foraging rhythms of both species and compared their foraging strategies. *Colletes cunicularius* started provisioning trips earlier in the morning, made more trips per day than *A. vaga*, and finished nest provisioning later in the evening. *Colletes cunicularius* burrowed even in the dark after 08.00 p.m. *Andrena vaga* collected pollen and nectar on different days each. One pollen day included 1 to 5 pollen trips. There was no clear correlation between the number of pollen trips and the occurrence of a subsequent nectar day. We found also no correlation between the occurrence of nectar-provisioning trips and weather conditions. Pollen loads of both species were analyzed qualitatively and quantitatively with a cell counter and two different hand-counting systems. *Andrena vaga* collected nearly twice as much pollen as *C. cunicularius* during one foraging trip. Cells and pollen loads of *C. cunicularius* contained large portions of other pollen types, mostly Rosaceae such as *Prunus*, *Sorbus* and *Pyrus* or *Acer*, *Quercus* and *Ilex*. Thus, *C. cunicularius* is not oligoleptic as described in the literature. The percentage of pollen types other than *Salix* increased at the end of the flowering period of *Salix*, which indicates a resource restriction at the end of the season. The reproductive success of *C. cunicularius* measured by nest provisionment exceeded that of *A. vaga*, because of longer activity per day and digging activity in the evening.

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*Andrena vaga* (Panzer 1799) and *Colletes cunicularius* (L.) are univoltine, vernal solitary bees which are distributed throughout the entire Palearctic Region. They prefer to nest in sandy soils and often form large aggregations (Friese 1923, Moeschler 1938, Vleugel 1947, Westrich 1990). Both species are reported to be specialized on *Salix* as a pollen resource for their larvae (Westrich and Schmidt 1987). Being specialized on the same host-plant, their seasonal activity strongly overlaps (Westrich 1990). Therefore, we investigated the diurnal activity pattern and foraging strategy of both species. Several studies have dealt with diurnal activity patterns and the impact of weather conditions on a

number of mostly Nearctic bee species (cf. Batra 1999, Lind 1968, Michener and Rettenmeyer 1956, Schönitzer and Klinksik 1990, Stephen 1966), but precise data on the life cycle of European species of *Andrena* and *Colletes* are very scarce (Gebhardt and Röhr 1987, Malyshov 1927, Witt 1992).

By analyzing thoroughly the daily activity patterns, niche differences between two species may be shown. Levermann et al. (2000) investigated the diurnal cycle and niche differentiation of *Dasypoda hirtipes* (Fabricius) and *Panurgus calcaratus* (Scopoli). They demonstrated that apart from weather conditions, body mass and pollen-collecting apparatus are important factors

determining the diurnal activity cycle. Regarding solitary Hymenoptera, female size appears to have a great influence on provisioning- and reproductive success (Alcock 1979). *Colletes cunicularius* is larger than *A. vaga* and has more hairs, especially on the thorax. Therefore, we hypothesized that better thermoregulatory abilities allow *C. cunicularius* an earlier start to provisioning activity in the morning.

Apart from the different sizes of the two species, the specific pollen-collecting apparatus suggests differences in their pollen collecting efficiency. Although both species have trochanter-femur-baskets, floccus and thoracic pollen basket of *A. vaga* is more strongly developed than in *C. cunicularius*. In a number of bee genera, the size and the type of pollen-collecting apparatus results in different amounts of pollen transported (Brau   1916, Friese 1923, Michener et al. 1978, Pasteels and Pasteels 1979, Westerkamp 1987, 1996, Westrich 1990). Thus, we examined the number of collected pollen grains in both species.

Although both species are regarded as strictly oligolectic on *Salix* (Vleugel 1947, Westrich and Schmidt 1987, Westrich 1990), anecdotal observations reviewed by Mader (1999) suggest that *C. cunicularius* visits also flowers other than *Salix*. A clear evaluation about oligolecty in a bee species can only be made by a quantitative analysis of pollen loads or cell provisions.

The aims of this study were to analyze niche differentiation of two synchronous and syntopic bee species on the basis of activity patterns and the use of host plants, to asses the degree of oligolecty, and to compare their pollen collecting efficiency.

The study area is part of the so-called "Wahner Heide", a large 5000 ha heathland, east of the river Rhine near Cologne. Since 1961 the heathland has been a military training area for NATO and was designated a Nature Reserve in 1968. Due to the presence of Quaternary gravel, sand

and overlaying quicksand, soils are mostly sandy, permeable, and poor in nutrients. The climate is humid-oceanic with an annual mean temperature of 9.5 °C and an annual mean precipitation of 804 mm. Due to drainage and loss of traditional agricultural use, grass and bushland dominate great areas of the heathland (Interkommunaler Arbeitskreis Wahner Heide 1989). The investigated aggregations of *C. cunicularius* and *A. vaga* lie on sandy inland dunes.

## METHODS

*Field work.*—To study their diurnal activity, individual female bees were marked with opalith-plates. A total of 238 females of *C. cunicularius* in 1996 and 174 females of *A. vaga* in 1997 were marked. Corresponding nests were identified by a colored nail of the same number as on the opalith-plate of the female. To record the exact departure and return times of the females, several nests were covered with preserving jars (cf. Witt 1992).

Climatic parameters were measured with data loggers (Orion Tiny Logger Manager OTLM Tinytalk  ). Soil temperatures of all years were recorded 20 cm below the surface, and air temperature and atmospheric humidity in a portable weather station were measured at a height of 2 m in 1997–1999. Data from the Cologne/Bonn airport weather station were also used. The data on the activity and the nectar trip frequency of the bees were tested for possible correlation against various climatic parameters (daily hours of sunshine, mean daily temperature, mean daily atmospheric humidity, humidity of soil and minimal daily soil temperature).

Since the activity of most of the bees is extremely influenced by weather conditions (Larsson 1991, Lind 1968) we created a measure for the bees activity independent from weather conditions (cf. M  ller 1994), which we referred to a so-called "bee day" (= BD). Such a measure makes it also easier to compare different years.

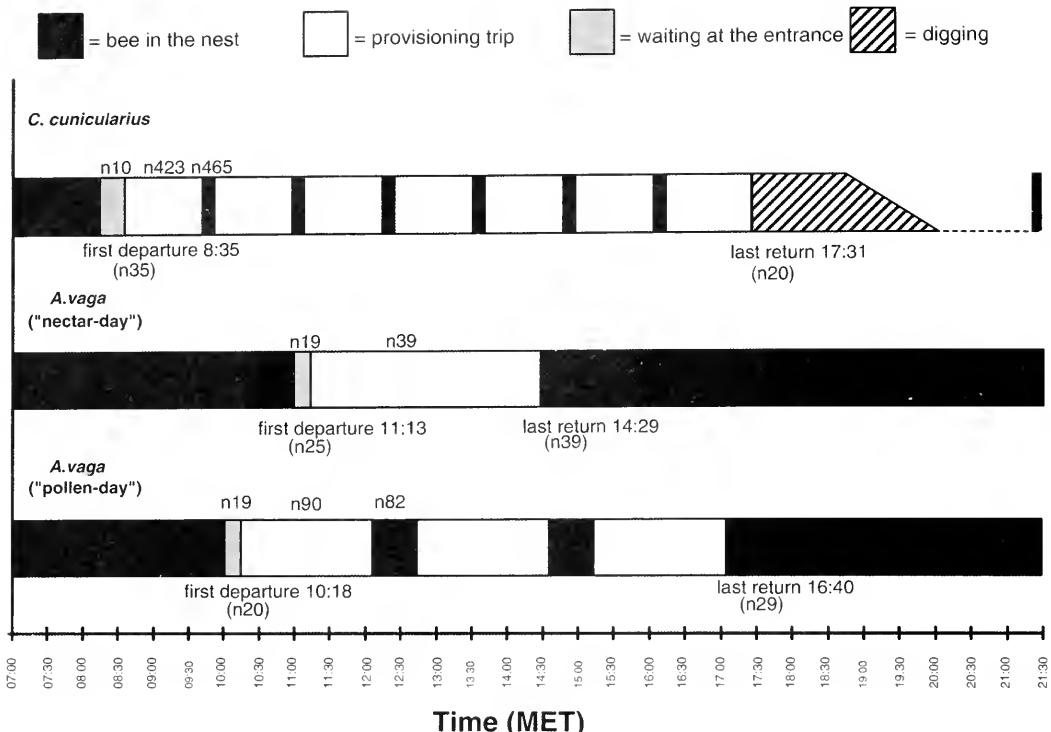


Fig. 1. "Ideal ethogram". Time schedule of provisioning behavior of *A. vaga* and *C. cunicularius* (dotted line = end of burrowing unknown). Further information's see text.

One bee day corresponds to a day with optimal weather conditions, which females could use completely for provisioning activities. A bee day for *C. cunicularius* had between 8–9 hours. The measure for these 8–9 hours was the observed flying activity at such an optimal day. Other days with less optimal flying conditions were defined as follows:

- 1.0 BD = flying activity of 8–9 hours
- 0.75 BD = flying activity more than  $\frac{1}{2}$  of one BD
- 0.25 BD = flying activity less than  $\frac{1}{2}$  of one BD
- 0 BD = no flying conditions the whole day

The classification of the bee day of *A. vaga* was more difficult because of the greater variance in activity time, in spite of good weather conditions:

- 1.0 BD = flying activity of 8–11 hours

- 0.75 BD = flying activity more than  $\frac{1}{2}$  of one BD
- 0.25 BD = flying activity less than  $\frac{1}{2}$  of one BD
- 0 BD = no flying conditions the whole day

*Nectar- and pollen days of A. vaga.*—To assess a pattern between *A. vaga*'s nectar- and pollen-provisioning trips, we analyzed the number of pollen days as well as the number of pollen trips between nectar trips. One nectar trip corresponds to one nectar day and the patterns of pollen trips between nectar trips occurs over a period days since pollen and nectar are collected on different days. We obtained complete observations of pollen trips between nectar trips of 7 different females.

*Pollen analysis.*—For pollen analysis we excavated 10 cells of *C. cunicularius* in 1996 and 6 cells in 1998. The cells could not be attributed to a specific nest or time of com-

pletion. Additionally, females were captured to analyze pollen loads. This was necessary for *A. vaga* because cells could not be excavated without destruction and partial loss of the pollen mass. A total of 38 pollen loads of *A. vaga* and 28 pollen loads of *C. cunicularius* were analyzed (see Table 1). To remove the complete pollen load from the bees, all body parts (legs and sometimes thorax without wings) were sonicated in vials filled with a liquid medium (cf. Buchmann and Shipman 1990). For a comparison of grain numbers, only pollen loads with nearly 100% *Salix* were used because the number of pollen grains varies with their size (see also Silveira 1991, Tasei 1973). For 10 pollen samples of *C. cunicularius* also volumetric percentages of the different pollen types were considered (cf. Buchmann and O'Rourke 1991). Pollen grain dimensions of *Salix*,

*Quercus robur* and *Prunus padus* were measured for 10 grains of each species under a scanning electron microscope (SEM). The average size of the grains of *Acer pseudo-platanus* were taken from Crompton and Wojtas (1993).

The number of pollen grains in cells and pollen loads was counted by different methods:

a) Ratio-counting with *Lycopodium* spores: For this quantification, pollen was acetolyzed (Erdtmann 1960, Moore et al. 1991). During acetolysis a tablet with a known number of *Lycopodium* spores was added (Stockmarr 1971). In a subsample all pollen grains and spores were counted on a slide under a microscope. The total number of pollen grains in the sample was estimated from the equation:

$$\text{total number of grains} = \frac{\text{added Lycopodium spores}}{\text{counted Lycopodium spores}} \times \text{counted grains}$$

b) Cell counter: Most of the samples were additionally analyzed using a cell counter (Casy® 1 Cell counter and Analyser) and then checked with the SEM. Eight electronically counted samples for the years 1996 and 1998 were checked with the *Lycopodium* spores method described above. Between 500 and 1000 *Salix* grains were counted, respectively.

c) Hand-counting with a counting chamber: Samples from 1999 were counted with a Buerker counting chamber, a special slide with a cavity of a defined volume. To achieve an accuracy of 10 or 20 grains per  $\mu\text{l}$ , we determined the number of subsamples needed using the following formula ( $n$  = random sample,  $s$  = standard error,  $d$  = accuracy):

$$n \geq \left[ \frac{1.96 \times s}{d} \right]^2$$

In this study, 6 to 14 subsamples had to be counted.

To calculate the number of provisioning trips for one cell, the average weight of food stored in the cell has to be divided by the average weight of the pollen load carried by the female (cf. Mohamed 1973). Therefore we determined the dry weight of the pollen load samples of the year 1996. The females were dried in a drying chamber, head and wings removed, and the rest weighted. Then pollen was removed from the body hairs and scopae with a sonicator. After removing the pollen, the thorax and abdomen were dried and weighed again. The difference corresponds to the weight of the pollen load.

**Statistics.**—Mean values of all departures and returns or other activities were used to construct an "ideal ethogram". Except in cases when data were not normally distributed, the median was used. The compari-

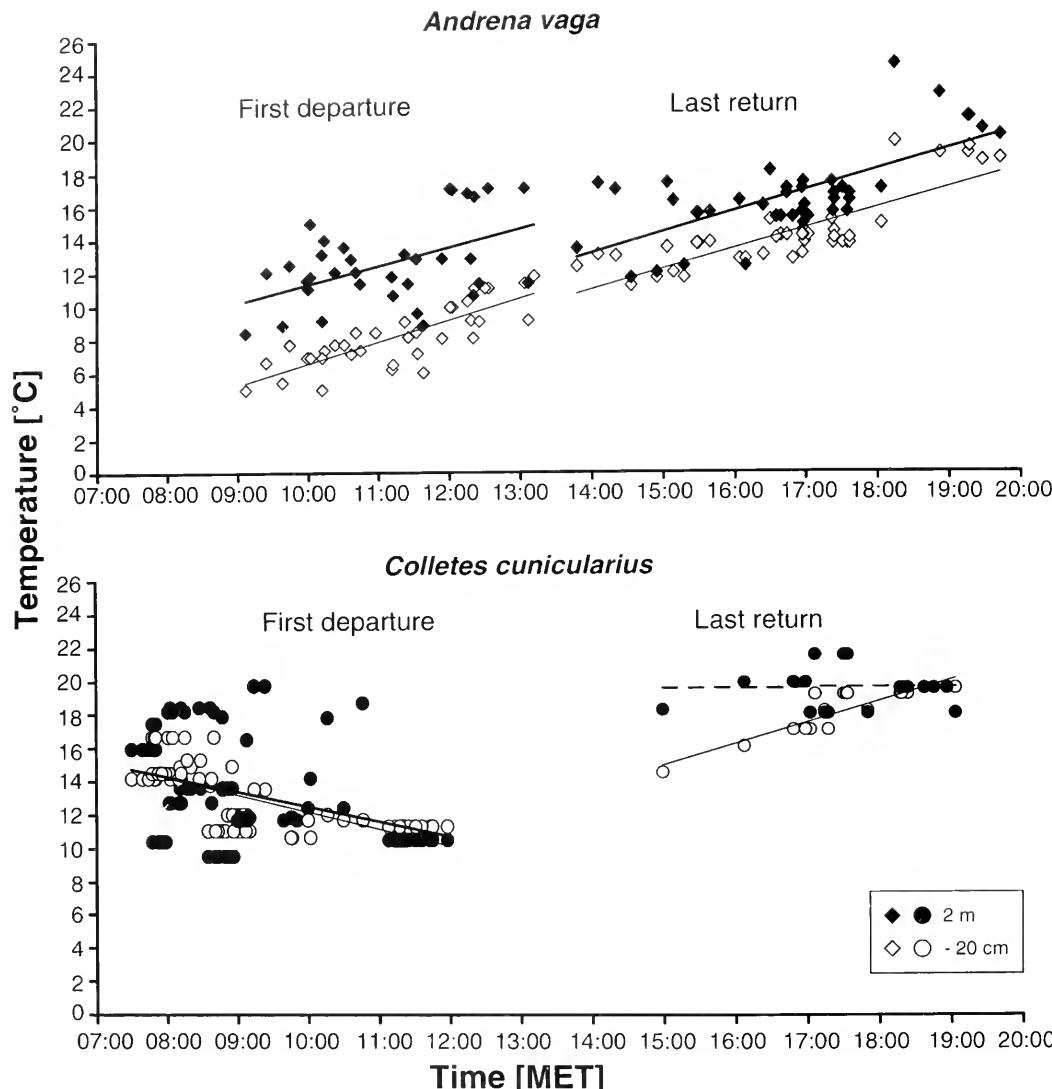


Fig. 2. Correlation of time of first departure and last return of *A. vaga* and *C. cunicularius* with temperature at 2 m height (BC = black circle; BS = black square) and 20 cm below soil surface (WC = white circle; WS = white square). (First departure: BS  $y = 26.49x + 0.21$ ,  $r = 0.48$ ,  $n = 36$ ; WS  $y = 30.92x - 6.38$ ,  $r = 0.82$ ,  $n = 38$ ; BC  $y = -21.57x + 21.45$ ,  $r = 0.36$ ,  $n = 78$ ; WC  $y = -24.56x + 22.37$ ,  $r = 0.71$ ,  $n = 78$ ; Last return: BS  $y = 29.94x - 4.31$ ,  $r = 0.68$ ,  $n = 42$ ; WS  $y = 29.35x - 6.16$ ,  $r = 0.81$ ,  $n = 42$ ; BC  $y = 0.34x + 19.25$ ,  $r = 0.01$ ,  $n = 20$ ; WC  $y = 30.12x - 3.88$ ,  $r = 0.89$ ,  $n = 20$ ).

son of mean values of activity data was presented in boxplots. These independent samples were analyzed with the t-test. Data of pollen samples were treated likewise. Mean values of non normally distributed data (number of pollen grains per pollen load and soil temperatures) were compared using the Man-Whitney U-test. The

relationship between activity data and climate and mixed pollen cells and the blooming time of *Salix* were tested by Pearson's correlation analysis.

## RESULTS

*Foraging strategy—diurnal cycle.*—A comparison of the “ideal ethogram” (Fig.

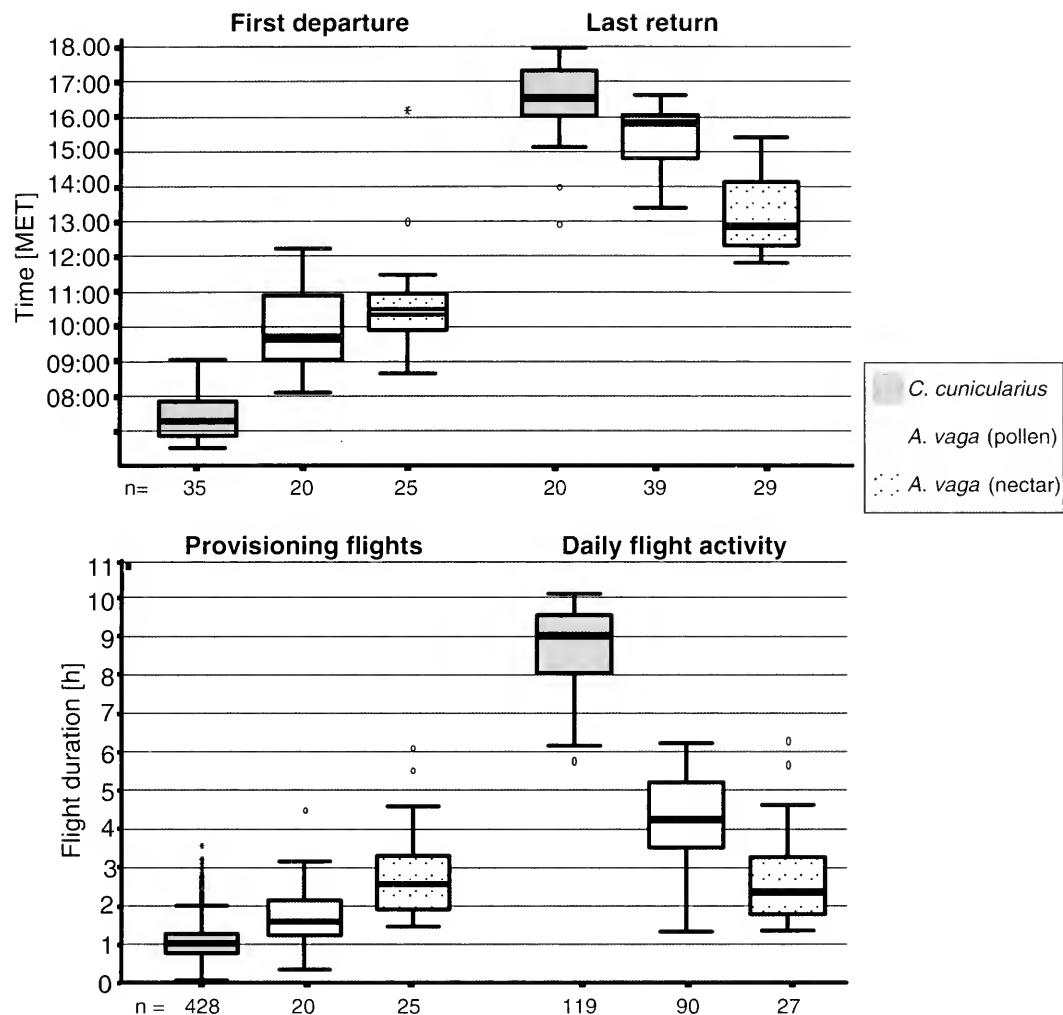


Fig. 3. Variance and difference in time of first departure, last return, time of provisioning trips and hours of daily activity of *A. vaga* and *C. cunicularius*.

1) shows a different diurnal cycle of *A. vaga* and *C. cunicularius*. For *A. vaga* two separate cycles are shown since it collects pollen and nectar on different days and this is represented by different flight patterns.

*Colletes cunicularius* started its first trip at 8:37 in the morning, after waiting about 20 minutes at the entrance. It made seven provisioning trips and returned from its last trip at 17:34. It did not interrupt its foraging cycle by digging or other activities in the nest, as indicated by short durations of presence in the nest (six minutes

on average). In the evening, after the last return to the nest, many females began burrowing and continued even in the dark (Fig. 1). *Colletes cunicularius* showed lower variation in the number of trips per day than *A. vaga*. The first departure and the last return of *C. cunicularius* correlated with the soil temperature (Fig. 2). The females started earlier when soil temperatures were higher and returned later from their last trip when temperature was still high. The correlation of the last return with the air temperature was not significant. The soil temperature at the aggre-

Table 1. Number of excavated cells and collected pollen loads (C. c. = *C. cunicularius*, A. v. = *A. vaga*).

Year	Cells C.c.	Pollen loads	
		C.c.	A.v.
1996	10	9	7
1998	6	1	14
1999		18	17

gation of *C. cunicularius* was significantly higher ( $U = 88698$ ,  $p < 0.001$ ) than the soil temperature of the location of *A. vaga*'s aggregation, though the year 1996 was much colder than 1997 (Bischoff 2000). Thus, lowest soil temperature during first departure of *C. cunicularius* ( $11^{\circ}\text{C}$ ) differed highly from soil temperature in the aggregation of *A. vaga* ( $5^{\circ}\text{C}$ ). The temperature threshold for the first trip of *C. cunicularius* was  $9.5^{\circ}\text{C}$ ; the mean temperature of first departure was  $12^{\circ}\text{C}$ .

On pollen days *A. vaga* made three trips on average. After remaining a while at the entrance, it started its first trip at 10:32. The females stayed on average half an hour (median 0.33) in the nest between two provisioning trips and no digging activity was observed during these periods. At 16:17 it came back from its last trip and closed its nest entrance. On nectar days, females emerged not before 11:30 and returned at 14:29. In the evening no intense digging activity as observed for *C. cunicularius*, occurred. The last return of the females was influenced by the temperature; a significant correlation of the time of the last return both with soil temperature and air temperature was found. The first flight in the morning, which started much later than that of *C. cunicularius*, seems not to be influenced by the temperature at all since a positive correlation was found (Fig. 2). The temperature threshold

for the first trip of *A. vaga* was  $8^{\circ}\text{C}$ , the mean temperature of first departure was  $12^{\circ}\text{C}$ .

To summarize, the females of *C. cunicularius* started their provisioning behavior earlier in the morning, made more but shorter trips a day, remained for shorter periods in the nest, returned later in the evening (Fig. 3) and burrowed after dark. *Andrena vaga* started its first trip later in the morning but the temperature threshold for the first trip was lower than that of *C. cunicularius*.

*Nectar and pollen days of A. vaga*.—*A. vaga* made 1 to 9 pollen trips between two nectar trips (mean: 4 trips, Table 2). Two groups of flight patterns seem to exist: the first group of bees makes 1 to 4 pollen trips between two nectar trips, and the second group makes 7 to 9 pollen trips between each nectar trip.

The activities of *A. vaga* females at different bee days are shown in Fig. 4. There was a high percentage of inactive females on 0.25 BD's, i.e. days with less than 5.5 hours of good flying conditions. On days with good flying conditions (1.0 BD), more females made pollen trips than nectar trips. Yet, this relation was also found on 0.25 BD's. Furthermore we compared the percentage of nectar trips with the bee day status of the preceding day. After a 0 BD (no flying conditions the whole day), females made significantly more often a nectar trip ( $r = -0.471$ ,  $p = 0.031$ ,  $n = 21$ ).

We also tried to correlate the percentage of nectar trips of *A. vaga* with climatic parameters of the same day and the preceding day (Table 3). At days with more hours of sunshine females made more often a nectar trip but the correlation was not very strong. Otherwise no significant

Table 2. Number of observed pollen trips between two nectar trips of *A. vaga*.

Pollen trips	1	2	3	4	5	6	7	8	9
Frequency	2	3	2	1	0	0	2	2	1

Table 3. Correlation (Pearson) of the percentage of nectar trips (of all active females of *A. vaga*) with climatic parameters of the day of the nectar trip (a) and of the preceding day (b) ( $n = 20$ ).

Day	Hours of sunshine		Mean temperature		Mean humidity		Minimum temperature	
	a	b	a	b	a	b	a	b
r	-0.578	-0.169	-0.86	0.76	0.308	0.244	0.302	0.113
p	**0.008	0.476	0.719	0.751	0.186	0.300	0.196	0.636

correlations with climatic parameters were found.

**Composition of pollen loads.**—In 1996, 40% of all analyzed cells of *C. cunicularius* contained more than 20% of pollen types other than *Salix*. Since only percentages of foreign pollen types lower than 5% (Westrich 1990) are considered as contamination, we decided to analyze more cells of *C. cunicularius* and pollen loads of *A. vaga*. In subsequent years, high percentages of non-*Salix* pollen were identified in the cells of *C. cunicularius*. In fact three of six excavated cells in 1998 and one of 10 cells in 1996 respectively, contained no *Salix* pollen at all. Only three cells of both years were pure ( $>90\%$  *Salix*) and 9 cells were mixtures of *Salix* and other grain types. The remaining pollen types in the cells of 1996 were mainly composed of various Rosaceae (Table 4). Apart from Rosaceae, only *Quercus* and *Sambucus* occurred in higher percentages. *Ilex* pollen dominated one pollen load sample of *C. cunicularius* of 1996.

Percentages of other pollen types were also found in pollen loads of *C. cunicularius* of the years 1998 and 1999. The loads of two females (captured on 29.4. and 7.5.1999) contained only grains of *Acer* sp., one load (also from 7.5.1999) contained *Acer* and *Ilex* grains in a ratio of 1:1, and two pollen loads contained exclusively *Quercus* pollen. Regarding also the volume of the different pollen types (10 samples of 1999), *Salix* grains represent even a smaller proportion of the diet of *C. cunicularius*, since *Acer pseudo-platanus*, *Prunus padus* and *Quercus robur* grains are much larger than *Salix* (Fig. 5). Percentages of

other pollen types in pollen loads of *C. cunicularius* (in the year 1998) increased significantly with time, i.e. with the end of the blooming of *Salix* ( $r = 0.731$ ,  $p = 0.01$ ,  $n = 14$ ).

In the graphs of the cell counter (Fig. 6), mixed loads of mainly two pollen types (*Salix* and various Rosaceae) could be recognized as two separated peaks. These graphs are counts from *C. cunicularius* cells of 1999. They show three clearly separated peaks. The first peak represents particles smaller than 10  $\mu\text{m}$  and can be interpreted as pollution. The second peak (15–22  $\mu\text{m}$ ) represents the *Salix* grains. The third peak (25–35  $\mu\text{m}$ ) shows bigger grains, e.g. Rosaceae. The broad distribution of grain sizes as displayed in the counter graph corresponded to different pollen types detected under the light microscope. However, results of the hand countings differed often from percentages given by the counter. All results of the counter had to be checked at least qualitatively by microscope, because one peak could represent pollen types other than *Salix*.

The cell counter calculated a mean number of 1512901 ( $\pm 720715$  SD) pollen grains per pollen load for *C. cunicularius*. Only 7 out of 18 pollen loads counted by the cell counter were pure *Salix* loads. In *A. vaga*, electronic counting determined 2058692 ( $\pm 737197$  SD) grains per pollen load. *Andrena vaga* collected on average one and a half more pollen on one provisioning trip than *C. cunicularius*. This difference is highly significant ( $t$ -test,  $p < 0.001$ ).

A comparison of the results using different counting methods is displayed in

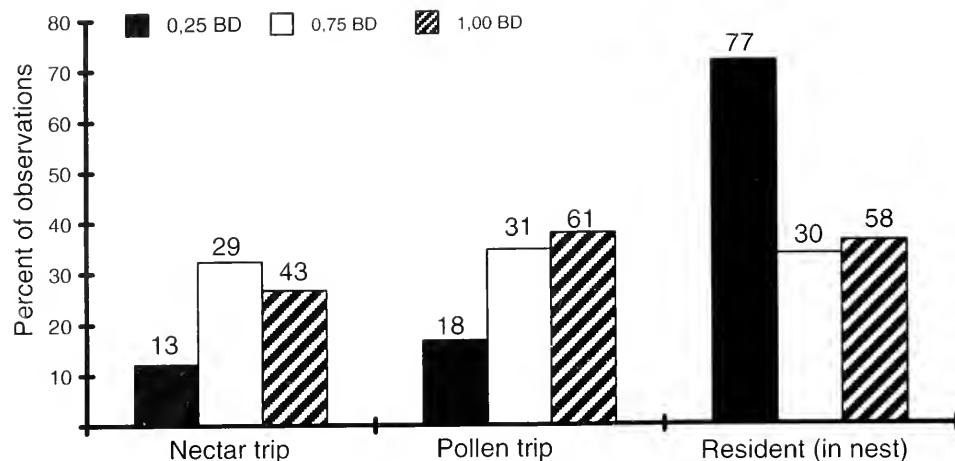


Fig. 4. Activities of *A. vaga* females at a bee day of the category 0,25 (< 5,5 hours good flying-conditions), a bee day of the category 0,75 (> 5,5 hours good flying conditions) and the category 1 (8–11 hours good flying-conditions) (number of total observations = 360).

Table 5. Ratio counting with *Lycopodium* spores showed greater divergence from cell counter results than counting with the counting chamber. Counting chamber results revealed a mean difference of 255728 ( $\pm 192194$ ) grains in comparison to the cell counter. Regarding *Lycopodium* ratio counting, one half of the results exceeded the cell counter calculations and the other half was below the cell counter calculations. The mean difference between *Lycopodium* spores ratio counting and cell counter was 498713 ( $\pm 675670$ ) grains.

The pollen loads of *A. vaga* contained fewer foreign grains than those of *C. cunicularius*. In five (13%) of 38 loads, we found percentages of other pollen types

ranging from 1 to 7% and consisting mostly of Rosaceae, *Quercus* and *Betula* grains.

## DISCUSSION

*Diurnal cycle—foraging strategies.*—In this study, *C. cunicularius* started its provisioning cycle much earlier than *A. vaga*. The specified activity times are probably dependent on weather conditions. This earlier departure may have been caused by higher soil temperatures. However, the departure time is not known from the other study site at the Fliegenberg. The investigated aggregation of *C. cunicularius* is exposed southward, has a strong slope and the soil is only sparsely covered with vegetation. The exposition of *A. vaga*'s ag-

Table 4. Classification of pollen types other than *Salix* in the cells of *C. cunicularius* in 1996.

Family	Genus or species	Percentage [%]
Rosaceae	<i>Sorbus aucuparia</i> , <i>Prunus padus</i> , <i>Prunus laurocerasus</i> , <i>Prunus</i> sp., <i>Pyrus</i> sp., <i>Malus</i> sp.	5–92
Fagaceae	<i>Filipendula</i> sp.	<1
Caprifoliceae	<i>Quercus</i> sp.	2–10
Ranunculaceae	<i>Sambucus nigra</i>	7
Celastraceae	<i>Ranunculus</i> sp.	0.2–3.3
Aceraceae	<i>Euonymus europaeus</i>	2
	<i>Acer</i> sp.	<1

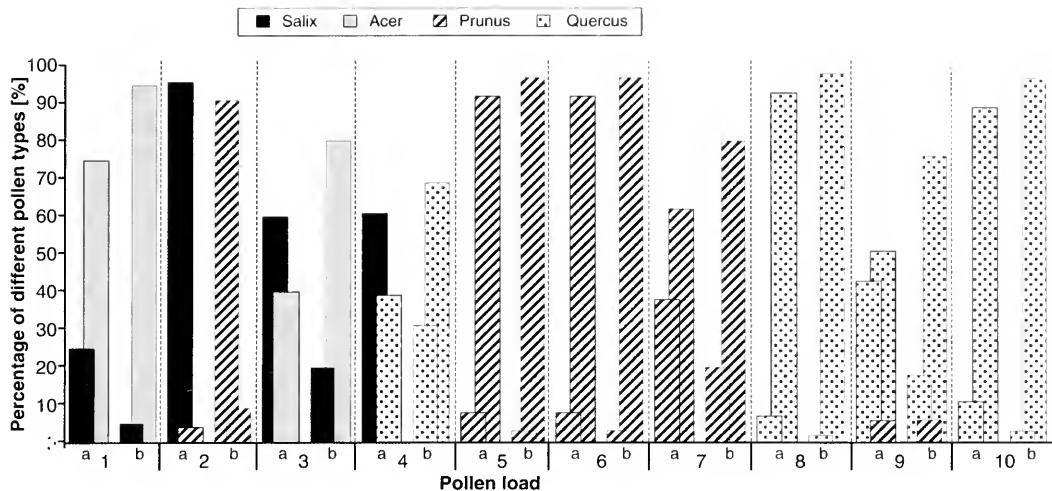


Fig. 5. Numerical (a) and volumetric (b) percentage of *Salix* pollen and other pollen types in excavated cells of *C. cunicularius* in the year 1996 and 1998.

gregation is south-eastward, slope is lower than in the *C. cunicularius* aggregation and the sand path is covered with grass. The surrounding site of *A. vaga*'s aggregation has also more and higher vegetation cover. Thus, higher soil temperature at the *C. cunicularius* aggregation may be caused by these local differences of exposure, slope and vegetation cover (cf. Bischoff 2000). Ideally, the diurnal cycle of *C. cunicularius* should be investigated at aggregations close to *A. vaga*'s aggregation, i.e. with similar conditions of soil, exposure, slope and vegetation cover.

Several authors have found correlations between the behavior of bees and weather conditions (e.g. Linsley 1958, Michener and Rettenmeyer 1956, Willmer 1983). Temperature thresholds for the bee's activities depend on weather conditions and the season in which the species occurs. Many vernal bees begin flight activity at 10 °C and they are less influenced by cloud cover or wind. Flight activity temperatures reported for other European early spring species of *Andrena*, for instance *A. barbilabris* (Kirby), *A. cineraria* (Linnaeus), *A. clarkella* (Kirby), and the Nearctic species *A. erythronii* Robertson, *A. viburnella* Graenicher, and *A. vicina* Smith range

from 10 to 16 °C (Gebhardt and Röhr 1987, Johnson 1981, Michener and Rettenmeyer 1956, Miliczky and Osgood 1995, Stephen 1966, Witt 1992). For vernal species of *Colletes* like *C. inaequalis* Say and *C. validus* Cresson, similar temperature thresholds are known (Batra 1980). In our study, the two species began flight activity at 8–9.5 °C air temperature. Similarly, Schönitzer and Klinksik (1990) recorded flight activity at a temperature of 8 °C for *A. nycthemera* Imhoff. Due to unstable weather conditions in spring, vernal species have to use days with good weather conditions very efficiently. To illustrate, on days with optimal weather conditions provisioning activity of *A. clarkella* is completed in 4 or 5 days (Friese 1923). Late summer species such as *Panurgus banksianus* (Kirby) and *Dasyopoda hirtipes* (Fabricius) often need temperatures > 20 °C to start their first trip (Lind 1968, Münster-Swendsen 1968). Though the flight of *A. vaga* may already start at 8 °C, time of its first departure is later than that of many of the other species of *Andrena* mentioned above. This may be caused by local and seasonal differences in temperature compared to the other studies mentioned above. In the present study the required temperature threshold of 8 °C

at the investigated aggregation of *A. vaga* was not reached before 09.00 a.m. This fact may explain the strange correlation of the first departure of *A. vaga* with the temperature, which represents in fact no correlation with the temperature. The bees can start their first trip at a temperature threshold of 8 °C and the regression represents only the increasing number of starting bees with time.

Apart from differences in soil temperature, the beginning of flight activity of the two species may be influenced by their respective thermoregulatory abilities. Larger bees are more likely to achieve flight temperatures at low ambient temperatures (Michener and Rettenmeyer 1956, Stone et al. 1988, Stone and Willmer 1989, Stone 1993a, b, Stone 1994, Stone et al. 1995, Wolda and Roubik 1986). *Colletes cunicularius* is one of the largest bees in Germany, having a mean heating rate of 7.35 °C per minute (Stone and Willmer 1989). These authors investigated the heating-rate among *A. clarkella* and *A. fulva* (Müller). These two species are comparable to *A. vaga* in body size, hairiness and flight season, and differ only in color from *A. vaga*. Mean heating rate of these two species of *Andrena* is about 4 to 6.2 °C per minute, respectively. Although *C. cunicularius* is larger and more hairy than *A. vaga*, the abdomen of the latter is deep black and passive heat absorbency may be increased. Nevertheless, body size is probably more important for warming up in the morning and may enable *C. cunicularius* to begin earlier with daily activity. After sunset, this species may also benefit from its larger size.

Most of the flights of *A. vaga* took between 1 and 2.5 hours on pollen days, and between 2 and 3.5 hours on nectar days. The known duration of provisioning trips of other species of *Andrena* ranged from 20 minutes to 4 hours, and the number of provisioning trips per day showed a transition from 1 to 5 (Gebhardt and Röhr 1987, Michener and Rettenmeyer 1956,

Miliczky and Osgood 1995, Schönitzer and Klinksik 1990).

A second reason for the marked difference in daily activity of the two investigated species could result from *A. vaga*'s prolonged stay in the nest. It could not be clarified whether *A. vaga* uses these periods in the nest for digging, since no new sand was pushed to the surface. The occurrence of sand output depends of the sequence of nest construction. When the bee first digs the main burrow and constructs the cells regressively (i.e., the lowest one is built first and each subsequent one is at a higher level), it can fill the inferior main burrow with the material of the side burrows. Thus no new sand needs to be pushed out. This has been described by Malyshев (1927) for *C. cunicularius* and also by Rajotte (1979) for *C. validus*. Yet, *A. vaga* constructs its nest conversely, subsequent cells lie deeper and the oldest cell is nearest to the surface. Side burrows of *A. vaga* are also filled with sand and in order to fill the first side burrow of a completed cell, the bee may use the material of a second side burrow. This was also assumed by Michener and Rettenmeyer (1956) for *A. erythronii*. Our (Bischoff 2001) and Malyshev's (1926) description of *A. vaga*'s nest architecture are contradictory to the descriptions and figures of Friese (1882, 1923), in which the last cell is located at the lowest level. Michener and Rettenmeyer (1956) suggested that Friese's nest figure with cells close along the main burrow like a cluster of grapes resulted from a mixture of different nests lying very close together.

In many species, digging of side burrows and new cells has been described to take place in the afternoon (Lind 1968, Münster-Swendsen 1968, Gebhardt and Röhr 1987, Michener and Rettenmeyer 1956, Witt 1992). However, our results do not confirm these findings for *A. vaga*, where even after the last provisioning trip, females did no intensive digging as observed in *C. cunicularius*. Yet, at the begin-

Table 5. Results of pollen counts with the electronic counter, the counting chamber and the Lycopodium-ratio-method (means of all counts of both species).

	Grain number/pollen load	Standard deviation	Mean difference to electronic counter
Electronic counter	1053796	722183	
Counting chamber	1777806	626778	255728
Lycopodium-ratio-counting	798069	711542	
	1850200	515579	498713

ning of the season, when the aggregation of *A. vaga* develops, new tumuli could be found early in the morning. Thus, we assume that the construction of these tumuli took place at night or early in the morning, because sand often was still moistened and no sand output was observed in the late evening of the previous day. *Andrena erythronii* digs in the late afternoon and even in the dark (Michener and Rettenmeyer 1956). Nocturnal digging activity has been reported from other Nearctic species of *Colletes* (Batra 1980, Rajotte 1979). Since *C. cunicularius* constructs its cells regressively as described above, no large sand output should occur after the construction of the main burrow. Digging activities in the evening can be interpreted as constructions of new nests, since *C. cunicularius* makes 2 or 3 nests in its life. *Colletes cunicularius* defers the construction of new nests to the evening time, thus it can use the whole day for provisioning trips and can increase the number of constructed nests.

The third explanation for the difference in daily activity may be the different pollen carrying capacities of both species. Brau   (1916) and Friese (1923) described the different pollen collecting apparatus of bees and inferred from these differences the systematic order of bee genera. Since these early studies, many authors worked on different pollen collecting apparatus (Grinfeld 1962, Michener et al. 1978, Pasteels and Pasteels 1979, Proctor et al. 1996, Thorp 1969, Westerkamp 1987). According

to Brau   (1916), *Andrena* is the genus that can carry home the largest amount of pollen with its hind leg brushes and parts of the thorax. Although both species have trochanter-femur baskets, the floccus and thoracic pollen baskets of *A. vaga* seem to be more strongly developed than in *C. cunicularius*. In the present investigation, *A. vaga* collected nearly twice as much pollen per load on average than *C. cunicularius*. Exact quantitative data on number of pollen grains per pollen load are scarce in the literature. In most cases, only percentages of different pollen types are presented, e.g. pollen loads of *Andrena* (Chambers 1946). Parker (1981) analyzed pollen loads of polylectic and oligolectic bee species quantitatively in order to determine the effectiveness of these species in pollinating sunflowers. He demonstrated that female oligoleges carried more pollen than did any other group of bees studied. In our study, species collected much more grains per load than in Parker's example; however, the number of carried pollen grains depends highly on the mean size of the grain type. Accordingly, our results can only be compared quantitatively to data of the same bee species, collecting the same pollen species. One possible factor as to why *C. cunicularius* pollen loads were smaller than *A. vaga*'s is that *C. cunicularius* collects nectar along with pollen in each trip. From honey bees and bumble bees it is known that they can carry an amount of nectar from 50 to 90% of their body weight (Heinrich 1979). We

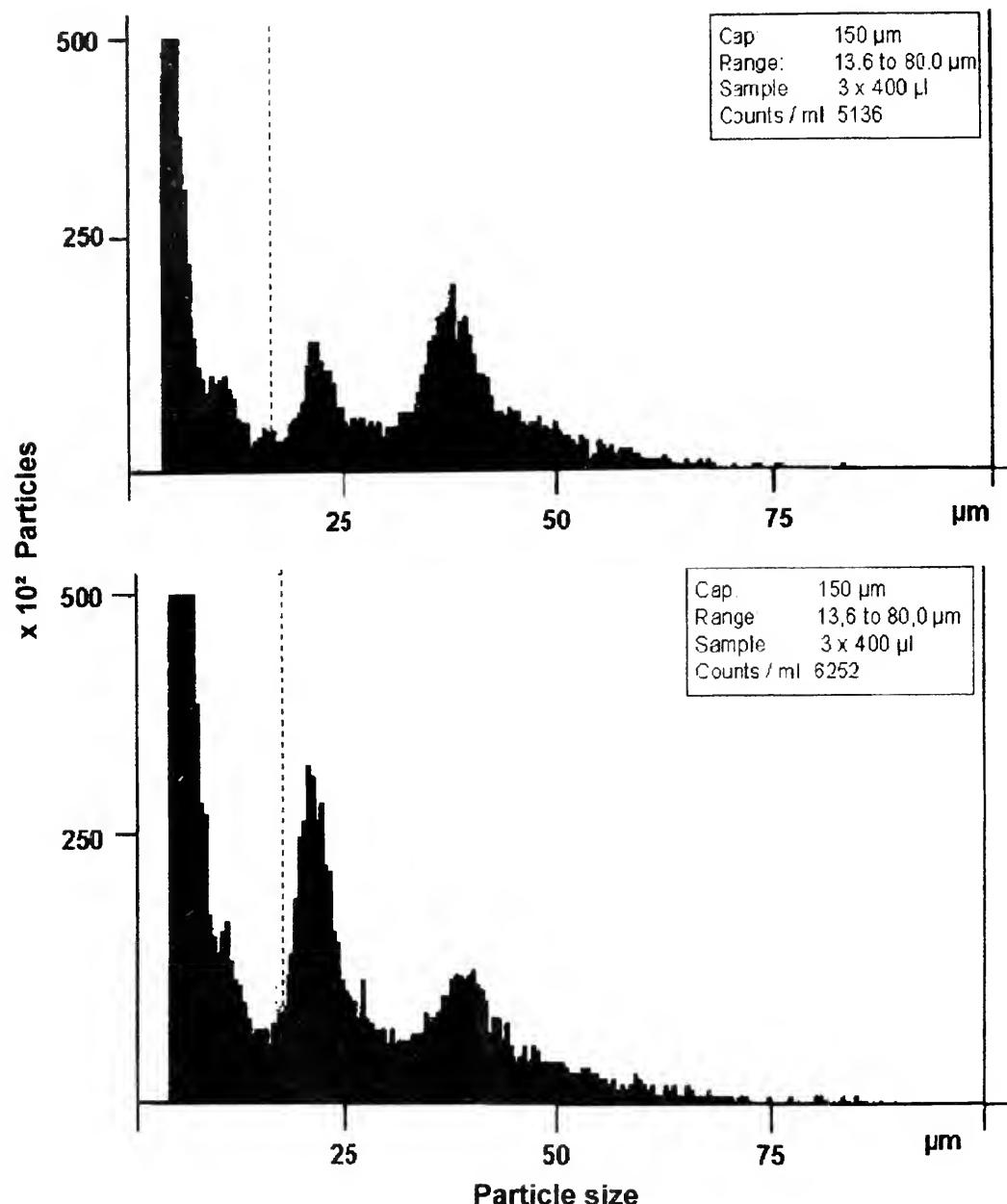


Fig. 6. Quantitative analysis of the pollen loads of *C. cunicularius* with the cell counter. Upper graph: 1. female, 23.04.99, below: 2. female, 27.94.99 (Cap = capillary, particles beneath dotted line = smaller than 10  $\mu\text{m}$ , no pollen).

were unable to find precise data in the literature on the amount of nectar collected by solitary bees on one single trip, but for *C. cunicularius* it is reported that the provision in the cell is extremely liquid and

though contains a lot of nectar (Malyshev 1936). Other bees like *Osmia rufa* (Linnaeus) make more dry provisions (Westrich 1990).

Dividing the grain number of the pure

*Salix* cells for the year 1996 by the grain number of pure *Salix* pollen loads (same year), *C. cunicularius* had to make approximately nine provisioning trips per cell. In 1998, we had only one cell of *C. cunicularius*, containing only *Salix* grains. In this case, *C. cunicularius* had to collect seven pollen loads for completing one cell. If *A. vaga* had to gather approximately the same amount of pollen per cell, it would have to make only four trips per cells, because of its bigger carrying capacity per load. These assumptions agree well with the observed trips of both species during one day. Vleugel (1947) observed for *A. vaga* only 1 or 2 trips on days with good weather conditions. The foraging statistics for *Andrena complexa* visiting *Ranunculus* for pollen show a time of 1½ hours to complete a load, and a pollen foraging rate of three loads per day (Linsley and MacSwain 1959). Furthermore the amount of pollen per cell may depend on the sex of the offspring. Gerber and Klostermeyer (1970) provided evidence that females determine the sex of their offspring by fertilizing the egg or not. Males are often smaller than females and therefore the stored pollen mass for males is smaller (Helms 1994, Strickler 1982, Maddocks and Paulus 1987, Johnson 1988). Regardless of the sex of the offspring, it seems likely that *C. cunicularius* has to make more provisioning trips per cell, because of its smaller pollen carrying capacity. In conclusion, *A. vaga* can carry more pollen per collecting trip; however, due to its body size *C. cunicularius* is more independent of weather conditions and can be active for longer periods per day. Indeed, the last point is of considerable importance for vernal bee species, because weather conditions are often quite unfavorable during spring. Additionally, *C. cunicularius* uses the evening and perhaps the night for digging activity. Our investigations of daily collecting capacity as well as those of nest excavations (cf. Bischoff 2001) indicate a higher reproduction

rate for *C. cunicularius* in comparison to *A. vaga*.

*Nectar- and pollen provisioning trips.*—We observed a rhythm of nectar and pollen provisioning trips and assumed that *A. vaga* collected first all the pollen for one cell, then added the nectar. Friese (1923) described exactly this type of behavior for *A. vaga*. *Dasyprocta hirtipes*, *Andrena erythronii* and various species of *Anthophora* are also known to add nectar only after several pollen loads have been carried into the cell (Lind 1968, Michener and Rettenmeyer 1956, Müller 1884, Westrich 1990). Malyshev (1936) states that pollen predominates in the first load or even makes up the whole load and that the last load deposited in the cell usually consists mainly of honey. Other species clearly alternate nectar- and pollen provisioning trips, e.g. *Osmia adunca* (Panzer), *Osmia fulviventris* Panzer or *Chelostoma florisomne* (Linnaeus) (Brechtel 1986, Käpylä 1978, Westerkamp 1978, Westrich 1990). It is possible that digger bees and carpenter or mason bees differ with respect to this behavior. Miliczky and Osgood (1995) described four trips for *A. vicina* during which no pollen was collected (in comparison with 64 pollen-collecting trips) and interpreted them as adult feeding trips. Since we did not analyze quantity of nectar in *A. vaga*'s cells, it cannot be definitely clarified whether nectar trips are adult feeding trips or nectar provisioning trips for the offspring. Assuming that *A. vaga* cells contain nectar, then there must be a rhythm between nectar and pollen provisioning trips. The two observed flight patterns may represent the different provisioning behavior for female and male cells. However, in order to prove this hypothesis, a longer series of provisioning trips of a greater number of females have to be documented and the mass of provisioned pollen has to be analyzed for sex specifically.

Another reason for the observed pattern of pollen and nectar trips may be the in-

fluence of weather conditions. Our underlying hypothesis was that females make a nectar trip after a particular hot and dry day to increase humidity inside the cell. In fact, Stephen (1966) noted that the temperature at which flight activity was initiated in *A. viburnella* was a function of weather conditions of the previous day. Yet, we did not find any correlation of occurrence of nectar trips to the climatic parameters of the previous day. On the contrary, after a bad weather day (no flying conditions the whole day) more females made a nectar trip. This may be caused by an increased energy consumption after one day in the nest. Probably females provide themselves with nectar during their pollen collecting trips (male *Salix* plants also produce nectar).

**Oligolecty.**—Qualitative comparison of collected pollen of both bee species indicated important differences in diet breadth between the two species: *A. vaga* collected almost pure *Salix* pollen, whereas *C. cunicularius* collected also a high percentage of other pollen types. The fact that whole cells contained exclusively other pollen types indicates that females of *C. cunicularius* systematically collect pollen from other host plants. Early flowering, tree-like Rosaceae in particular seem to be of great importance to this bee species. Mader (1999) listed a number of species of *Colletes* having a relationship to Rosaceae. In fact, the Nearctic *C. thoracicus* Smith and *C. nigrifrons* Titus are even specialized on Rosaceae. In our study, we found also pollen loads containing only *Quercus*, *Acer* or *Ilex* pollen, indicating that not only Rosaceae can replace missing *Salix* plants. On the Turkish coast, *C. cunicularius* females were observed foraging on *Pistacia*; *Salix* did not occur at this location. In Italy, *C. cunicularius* females were observed exclusively on Fabaceae (Kuhlmann in litt.). The whole complex of species, subspecies and their host-plants seems not yet clear. Mader (1999) cited several authors which observed *C. cunicularius* on many other

flowers than *Salix*, but their reports contain no precise information whether these flower visits were for collecting pollen or nectar. In fact it is not proved at all that *C. cunicularius* is really oligolectic on *Salix*. Therefore it is not clear whether the collection of other pollen, as observed in this study, is a result of resource restriction. The correlation of increasing percentages of other pollen types in the pollen loads of *C. cunicularius* with the end of flowering time of *Salix* may be an indication for a resource limitation. We registered all *Salix* trees within a radius of 3 km, most of which were *S. caprea*. In the years 1996 to 1998, these trees were blooming very early and had ceased to flower before females of *C. cunicularius* and *A. vaga* began to collect pollen. Only several bushes of *S. auricula* were available during nest provisioning time of both species. To prove whether *C. cunicularius* collects only other pollen when *Salix* is not available, comparative studies with resource quantifications at other locations from different years are needed.

In conclusion, *C. cunicularius* can not be regarded as an oligolectic species. The use of other, longer blooming host plants, which are more abundant in the study area, may increase the reproductive success of this species. In contrast to *C. cunicularius*, *A. vaga* seems not to be affected by the problem of long searching times for pollen sources, since it collected only *Salix* pollen. However, the activity time of *A. vaga* ceased approximately 4 weeks before that of *C. cunicularius* and the problem of pollen availability probably did not yet occur.

**Niche differentiation.**—*A. vaga* and *C. cunicularius* use the same host plant. This overlap may result in interspecific competition, if resources are limited. Since availability of specific pollen is one of the most relevant niche parameters for bees (Eickwort 1973, Strickler 1979), interspecific competition in case of a resource restriction seems very likely. Niche differ-

entiation is often the basis for the coexistence of competitors. There are a number of ways in which niches can be differentiated. In this case the niches of the two species seemed to be differentiated on the basis of conditions. This means that they use the same resource but their ability to do so is influenced by environmental conditions and they respond differently to these conditions (Begon et al. 1990). The two species show diurnal differences in their foraging behavior. This temporal separation is influenced by climatic parameters such as temperature.

Whether *C. cunicularius* uses other host plants because of resource restriction and/or competition with other species (besides *A. vaga* two other *Andrena* species specialized on *Salix* occur in the study area) or whether it is not oligolectic at all can only be proved with removal experiments and manipulation of the resource availability.

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## Taxonomic Revision of the Genus *Sesiocionus* Viereck (Hymenoptera: Braconidae: Agathidinae)

ROSA A. BRICEÑO G.

Universidad Centroccidental "Lisandro Alvarado", Decanato de Agronomía,  
Dpto. de Ciencias Biológicas-Sección Entomología, Tarabana, Cabudare,  
Estado Lara, Venezuela, e-mail: rabricen@telcel.net.ve

**Abstract.**—The Neotropical genus *Sesiocionus* Viereck and its type species *S. parathyridis* Viereck, are redescribed. Descriptions for twenty-six new species are presented: *S. acrolophus*, *S. amazonensis*, *S. ammosakron*, *S. analogus*, *S. areolatus*, *S. ariasi*, *S. armandoii*, *S. biospleres*, *S. boliiviensis*, *S. brasiliensis*, *S. chaconii*, *S. chrestos*, *S. clavijoi*, *S. diazi*, *S. dichromus*, *S. dominicus*, *S. eumenetes*, *S. galeos*, *S. garciai*, *S. grandis*, *S. kompsos*, *S. miyayensis*, *S. peruviensis*, *S. qui*, *S. theskelos*, and *S. venezuelensis*. Seventy-six morphological and color characters are discussed. A key to species is presented.

*Sesiocionus* Viereck 1912 is a Neotropical genus of the subfamily Agathidinae that, together with the genus *Earinus* Wesmael, comprise the tribe Earinini (Sharkey 1992). Viereck proposed *Sesiocionus* for the unique species described so far: *Sesiocionus parathyridis* Viereck.

The main characters that diagnose *Sesiocionus* are: tarsal claws simple, and notauli absent (Viereck 1912; Sharkey 1997). Many members of *Sesiocionus* have showy color patterns with body size varying between 3.0–12.0 mm. Despite the vivid color patterns and relatively large size, this genus is poorly represented in insect collections, and there is little biological information. Most species of *Sesiocionus* have been collected from November until March and between 100–2000 meters above sea level. Almost all specimens were collected in Malaise traps.

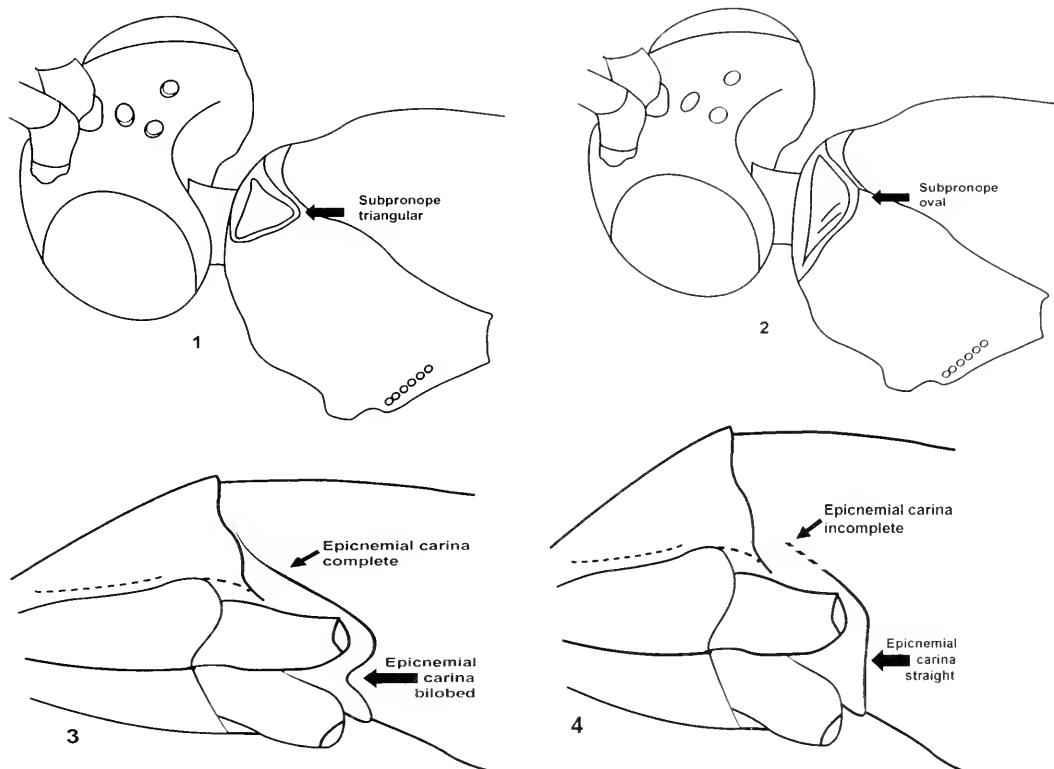
All known agathidines are parasitoids of Lepidoptera larvae (Sharkey 1988, 1997). The only previously known species of *Sesiocionus*, *S. parathyridis*, is recorded as a larval parasitoid of *Parathyris perspicilla* Stall (Lepidoptera: Arctiidae), although precise biology data (life cycle) are

not known (Viereck 1912, 1914). Sharkey (1997) estimated that this genus might include about thirty species and this revision includes a total of twenty-seven species.

### MATERIALS AND METHODS

Specimens are deposited in the following collections:

AEI: American Entomological Institute, Gainesville, FL, USA.  
BMNH: The Natural History Museum, London, England.  
CNC: Canadian National Collection, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, Canada.  
CUIC: Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, NY, USA.  
FML: Fundación Miguel Lillo, Instituto de Zoología Miguel Lillo, Tucumán, Argentina.  
INBio: Instituto de Biodiversidad, Santo Domingo, Heredia, Costa Rica.  
INPA: Instituto Nacional de Pesquisas da Amazônia, Depto. de Ecología e Biología Evolutiva, Universida-



Figs. 1-4. 1, Subpronope triangular in dorso-lateral view. 2, Subpronope oval-shaped in dorso-lateral view. 3-4, Epicnemial carinae. 3, Complete and bilobed. 4, Incomplete and straight.

de Federal de São Carlos, São Carlos, SP, Brasil.

MIZA: Museo del Instituto de Zoología Agrícola "Francisco Fernández Yépez", Universidad Central de Venezuela, Maracay, Aragua, Venezuela.

MZLU: Museum of Zoology, Lund University, Sweden.

TMB: Természettudományi Múzeum, Budapest, Hungary.

UCOB: Museo Entomológico "José M. Osorio", Universidad Centroccidental "Lisandro Alvarado", Tarabana, Lara, Venezuela.

UCR: Universidad de Costa Rica, San José, Costa Rica.

UK: Department of Entomology, University of Kentucky, KY, USA.

USNM: United States National Museum,

Smithsonian Institution, Washington, D. C. USA.

UWY: U. W. Insect Museum, University of Wyoming, Laramie, WY, USA.

ZSBS: Zoologische Sammlungen des Bayerischen Staates, Munich, Germany.

The revision was carried out at MIZA at the Universidad Central de Venezuela in Maracay, Venezuela.

Several morphometric characters were used in the descriptions and key. Measurements of *Body length* (mm) do not include the ovipositor. *Hind femur length and width* (Fig. 5) were measured in lateral view, with the length taken from the distal end of the trocantellus to the apex of the femur. The maximum width was measured, which is always near the midpoint. *First metasomal tergite length and width* re-

lationship (Fig. 7) refers to the median tergite with the length taken along the midline and the width measured at the apex. *Ovipositor length* (mm) was measured from the base of the hypopygium. In the description a measurement in parentheses following a range belongs to the holotype.

The terminology used for the carinae and areolae of the metanotum and propodeum follows Sharkey (1988), and the rest of the terminology, including wing venation follows Sharkey and Wharton et al. (1997). Additional terms used in this revision include the *occipital tubercles*, a pair of projections, one at each side of the occipital medial line (Figs. 16–18); and the *median areola of the metanotum*, which is the central area of metanotum often bordered with carinae (Figs. 25–29).

The key to *Sesiocionus* species was generated with the software DELTA version 4.07 (Dallwitz et al. 1997). Seventy six meristic, morphological and color characters were used for the matrix. The species descriptions also were generated with this software.

The biology for all the species described is unknown.

## RESULTS AND DISCUSSION

*Diversity and distribution of Sesiocionus.*—The genus is distributed from Southern Mexico to Southern Brazil. Members of *Sesiocionus* are poorly represented in entomological collections but most of these have been collected in Malaise traps in tropical localities between 0 and 1500 meters above sea level. Only *S. areolatus*, has been collected above 2000 meters, specifically at the Estación Biológica Las Alturas, in Costa Rica.

The poor collecting in many regions of the Neotropics may explain the scarcity of this genus in collections. This is clearly shown by the numerous specimens from Costa Rica and Panama where collecting has been extensive in recent years.

*Color patterns.*—Color patterns (yellow and black) shown by many braconids, in-

cluding *Sesiocionus*, are frequently shared with other orders of insects, specially Coleoptera and Hemiptera. However, some Lepidoptera, Neuroptera and Diptera also exhibit (Quicke 1997) these color patterns. Certainly, specimens of *Sesiocionus* could be confused with specimens of some of these groups when they are observed in nature, but the existence of a large mimetic complex has not yet been conclusively demonstrated. At taxonomic level, the various combination of yellow, orange, and black colors on the body of wasps are important characters for the separation of species.

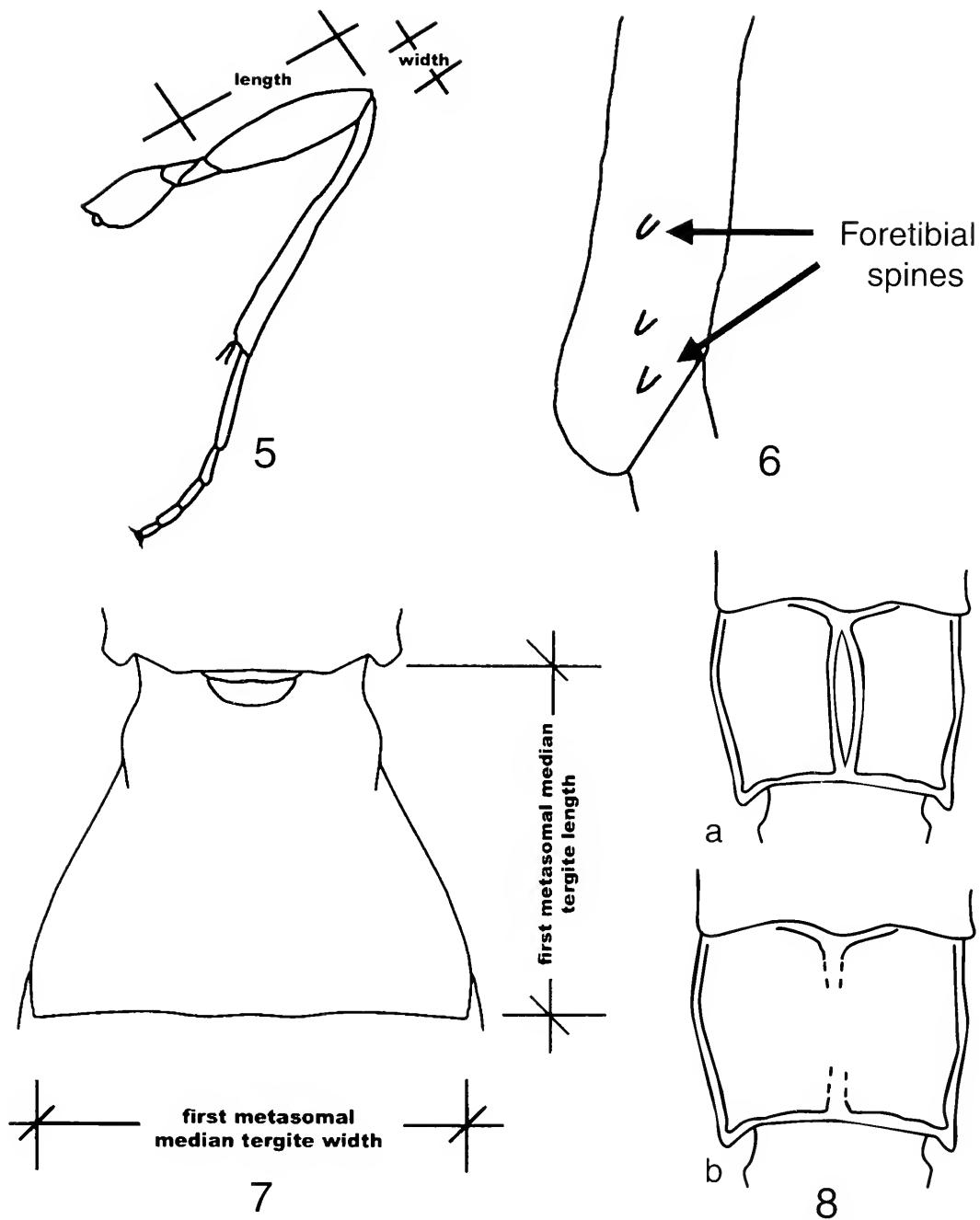
*Wing color pattern.*—The color pattern of the wings seems to be related to geographical distribution. Most species from South America have the wings banded from the base: yellow, infuscate, yellow, infuscate; while most species from Central America have the wings entirely infuscate. Another curious fact is that the only species from an island (*S. dominicus*) has hyaline wings. These observations could suggest that there are mimetic relationships with other insects on the continent, or perhaps the presence of a sham aposematic behavior, which was not present in the island.

## Genus *Sesiocionus* Viereck

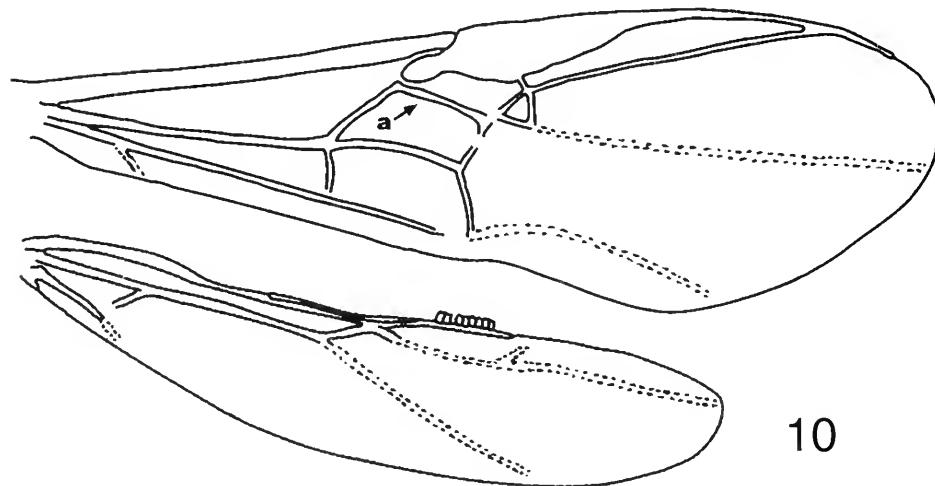
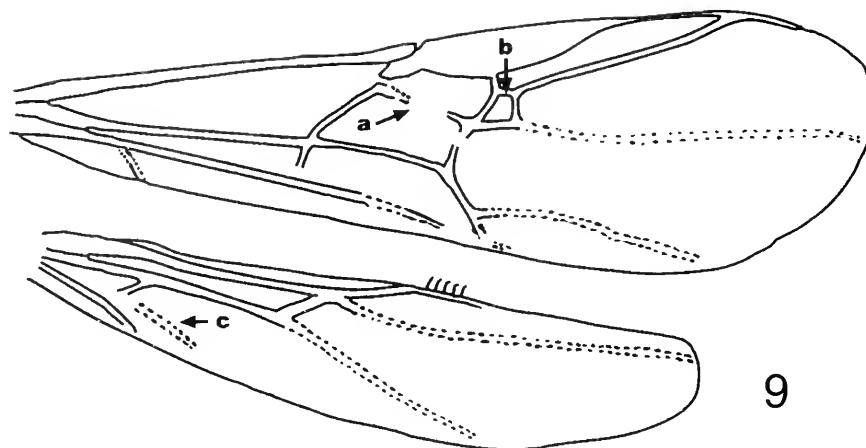
*Sesiocionus* Viereck 1912:1. Type species: *Sesiocionus parathyridis* Viereck. (Monobasic and original designation). Viereck 1914: 133.

*Diagnosis.*—*Sesiocionus* species may be distinguished from other agathidines using the following combination of characters: Body smooth and bright, lacking sculpture, scutellar depression smooth, notaui absent, tarsal claws simple (Fig. 32), epicnemial carina bilobed between fore coxae; rarely (8%) straight, ovipositor about as long as body length.

*Description.*—**Head:** Antenna with 23–48 flagellomeres, usually with 28–35; interantennal space with distinct keel (14%), or flat without distinct keel; antennal sockets



Figs. 5–8. 5, Hinged legs of Braconidae (Wharton et al. 1997) showing measurements done. 6, Apex of foretibia with spines. 7, First metasomal median tergite showing measurements done. 8, Propodeum, a, with central areola; b, without areola.



Figs. 9–10. Venation in *Sesioclonus*. 9, Forewing, a, (RS+M)a vein incomplete; b, 3RSa vein, hind wing; c, Cub vein not tubular. 10, Forewing, a, (RS+M)a vein complete.

excavated (51%); face rarely with longitudinal median carina; mandibles with two teeth, usually the outer tooth as long as the inner; maxillary palpus with four or five segments; labial palpus with three or four segments; third segment of labial palpus, when present, shorter and partially fused to fourth segment; gena usually moderately expanded posteroventrally (37%), sometimes not expanded; occipital tubercles often present (51%); occiput usually excavated. *Mesosoma*: Smooth and bright, without sculpture; subpronope tri-

angle-shape or oval-shape; notauli always absent; scutellum generally convex in lateral view, rarely flat; lateral carina of the scutellar depression usually absent; median areola of the metanotum often with longitudinal carina and lateral carinae that join posteriorly or not, generally smooth, sometimes with small rugosities; propodeum convex (49%) or flat (51%) in lateral view; longitudinal carina of propodeum usually absent, sometimes present; epicnemial carina absent (6%) or present (94%), complete (70%) or incomplete lat-

erally (24%), generally bilobed medially between fore coxae, sometimes straight; hind coxal cavities open, forming a common foramen with the metasoma; fore wing (RS+M)a vein present, complete (57%) or incomplete (43%); fore wing 3RSA usually present; hind wing with 3–10 hamuli, generally 4–6; hind wing 2-1A vein usually tubular; hind wing CUB vein not tubular; fore tibia sometimes with

spines; medial tibia usually with 2–16 spines; hind tibia with 5–25 spines, usually 12–17; tarsal claws simple on all legs.

**Metasoma:** Smooth and bright, without sculpture; median tergite of the first metasomal segment usually with two longitudinal dorsal carinae, rarely with pits posterad spiracle; ovipositor as long as length of the body. Length. 2.0–12.0mm; excluding ovipositor.

#### KEY TO SPECIES OF *SESIOTONUS*

1	Occipital tubercles present (Figs. 16–18) . . . . .	2
–	Occipital tubercles absent (Figs. 19) . . . . .	13
2(1)	Epicnemial carina straight medially or absent (indented at midline, between forecoxae), sometimes difficult to see (Figs. 4, 23) . . . . .	3
–	Epicnemial carina bilobed medially, (indented at midline, between the forecoxae) (Figs. 3, 22) . . . . .	5
3(2)	Epicnemial carina complete in lateral view (Figs. 3, 22) . . . . .	<i>garciai</i> sp. n.
–	Epicnemial carina incomplete or absent in lateral view (Fig. 23) . . . . .	4
4(3)	Face with median longitudinal carina (Fig. 13) . . . . .	<i>acrolophilus</i> sp. n.
–	Face without median longitudinal carina (similar to Figs. 12, 14) . . . . .	<i>analogus</i> sp. n.
5(2)	Midcoxa not completely melanic, color variable . . . . .	6
–	Midcoxa completely melanic . . . . .	7
6(5)	Fore tibia with spines (Figs. 6, 30), midcoxa yellowish orange, forewing (RS+M)a vein complete (Fig. 10a) and 3RSA vein present (Fig. 9b) . . . . .	<i>peruviensis</i> sp. n.
–	Fore tibia without spines, midcoxa melanic dorsally and yellowish orange ventrally, forewing (RS+M)a vein complete (Fig. 10a) and 3RSA vein absent (Fig. 10) . . . . .	<i>chaconi</i> sp. n.
7(5)	Longitudinal carina of scutellar depression present . . . . .	<i>venezuelensis</i> sp. n.
–	Longitudinal carina of scutellar depression absent . . . . .	8
8(7)	Median areola of metanotum with longitudinal rugosities (Fig. 29), median tergite of first metasomal segment without pair of lateral longitudinal carinae (similar to Fig. 34), fore wing (RS+M)a vein complete (Fig. 10a) . . . . .	<i>kompsos</i> sp. n.
–	Median areola of metanotum smooth (Figs. 25–28) . . . . .	9
9(8)	Mesoscutum melanic . . . . .	10
–	Mesoscutum yellowish orange . . . . .	11
10(9)	Fore wing infuscate with large hyaline spot, metasoma reddish brown . . . . .	<i>brasiliensis</i> sp. n.
–	Fore wing either infuscate without hyaline spot or hyaline basally, infuscate apically, mesosoma melanic and metasoma yellowish orange . . . . .	<i>dichromus</i> sp. n.
11(9)	Median longitudinal carina of propodeum present and complete . . . . .	<i>ariasi</i> sp. n.
–	Median longitudinal carina of propodeum absent or incomplete . . . . .	12
12(11)	Subpronope triangular (Fig. 1), fore wing 3RSA vein absent (Fig. 10) . . .	<i>boliviensis</i> sp. n.
–	Subpronope oval-shape (Fig. 2), fore wing 3RSA vein present (Fig. 9) . . . . .	<i>diazzi</i> sp. n.

13(1) Occiput excavated (similar to Figs. 16–18) . . . . .	<i>eumenetes</i> sp. n.
– Occiput not excavated (Fig. 19) . . . . .	14
14(13) Median areola of metanotum with lateral carinae (Figs. 25–28), flagellum with less than 40 flagellomeres, interantennal space with a rounded longitudinal keel or keel absent (Fig. 12), never sharp; specimens with less than 8mm in body length . . . . .	15
– Median areola of metanotum without sharp lateral carinae (Fig. 29), flagellum with 40 flagellomeres or more, interantennal space with a sharp longitudinal keel (Fig. 11), specimens greater than 8mm in body length . . . . .	25
15(14) Median areola of metanotum with lateral carinae present and meeting posteriorly (Figs. 25, 26) . . . . .	16
– Median areola of metanotum with lateral carinae present and not meeting posteriorly (Figs. 27, 28) . . . . .	23
16(15) Epicnemial carina present (Figs. 3, 4) . . . . .	17
– Epicnemial carina completely absent . . . . .	<i>ammosakron</i> sp. n.
17(16) Epicnemial carina complete laterally (Fig. 3) . . . . .	18
– Epicnemial carina incomplete laterally (Fig. 4) . . . . .	21
18(17) Hind tibia melanic . . . . .	<i>amazonensis</i> sp. n.
– Hind tibia mostly yellowish orange . . . . .	19
19(18) Propodeum with central areola absent . . . . .	20
– Propodeum with central areola present (Fig. 8a) . . . . .	<i>areolatus</i> sp. n.
20(19) Flagellum with 32 flagellomeres, interantennal space with rounded longitudinal keel (similar to Fig. 12), hind tibia yellowish orange in basal half, melanic apically . . . . .	<i>miyayensis</i> sp. n.
– Flagellum with 25 flagellomeres, interantennal space without longitudinal keel, hind tibia mostly yellowish orange, melanic apically . . . . .	<i>clavijoi</i> sp. n.
21(17) Epicnemial carina straight medially (between forecoxae) (Fig. 4), body length less than 3mm . . . . .	<i>dominicu</i> s sp. n.
– Epicnemial carina bilobed medially (indented at midline, between forecoxae) (Fig. 3), body length more than 3mm . . . . .	22
22(21) Forewing (RS+M)a vein complete (Fig. 10a) . . . . .	<i>armando</i> i sp. n.
– Forewing (RS+M)a vein incomplete (Fig. 9a) . . . . .	<i>biospleres</i> sp. n.
23(15) Epicnemial carina present, complete or incomplete laterally (Figs. 3, 4) . . . . .	24
– Epicnemial carina completely absent . . . . .	<i>chrestos</i> sp. n.
24(23) Epicnemial carina straight medially (indented at midline, between forecoxae) (Fig. 4) . . . . .	<i>galeos</i> sp. n.
– Epicnemial carina bilobed medially (indented at midline, between forecoxae) (Fig. 3) . . . . .	<i>theskelos</i> sp. n.
25(14) Third and fourth labial palpomeres not fused, first metasomal median tergite with depression posterad spiracle (Figs. 36, 37) . . . . .	<i>grandis</i> sp. n.
– Third and fourth labial palpomeres fused, first metasomal median tergite with or without depression posterad spiracle . . . . .	26
26(25) First metasomal median tergite with depression posterad spiracle (similar to Figs. 36, 37) . . . . .	<i>qui</i> sp. n.
– First metasomal median tergite without depression posterad spiracle . . . . .	<i>parathyridis</i> Viereck

***Sesioctonus acrolophus* Briceño, sp. n.**  
 Figs. 11, 13, 15, 21, 23, 24, 25, 30, 32, 35

**Diagnosis.**—Face with median longitudinal carina, interantennal space with a sharp longitudinal keel and median areola of metanotum with median longitudinal carina. *S. analogous* is similar but can be distinguished by this combination of characters.

**Description.**—♀. *Length.* Body, 9–10 mm (9.5). **Head:** Flagellum with 32 flagellomeres. Interantennal space with sharp longitudinal keel. Antennal sockets deeply excavated. Face with median longitudinal carina. Genae strongly expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth longer than inner tooth. Maxilla with 5 palpomeres. Third and fourth labial palpomeres not fused. **Mesosoma:** Subpronope oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; with median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina present. Epicnemial carina blunt, incomplete dorsally, straight medially (between forecoxae). Foretibial spines present. Midtibia with 8 spines. Hind tibia with 11 spines. Hind femur 3.17 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing present. 2-1A vein of hind wing not tubular. CUB vein of hind wing not tubular. Hind wing with 4–5 hamuli (4). **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.09. Ovipositor 9–10 mm (9.2). **Color:** Head melanic except maxillary and labial palpomeres sometimes yellowish orange. Antenna melanic. Mesosoma yellowish orange. Forelegs melanic except coxae yellowish orange. Midlegs melanic except coxae sometimes yellowish

orange. Hindleg melanic except coxa and femur mostly yellowish orange, but melanic distally. Forewing yellow basally and infuscate apically. Stigma melanic, or yellowish orange. Hind wing yellow basally infuscate apically. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—*Holotype:* Costa Rica: ♀, CRI002 492066, Prov. Alajuela, sector Colonia Palmareña, 700m, oct.1996, G. Carballo (INBio). *Paratypes:* Costa Rica: ♀, Heredia, Est. Biol. La Selva, 50–150m, 10° 26'N 84° 01'W, 02 de Marzo 1993, bosque primario (INBio); ♀, R. San Lorencito, 900m, R. F. San Ramón, 5km N de Colonia Palmareña, Prov. Alajuela, 13–18 Junio.1993, (without abdomen) (INBio); ♀, Heredia, 3km S. Puerto Viejo, OTS, La Selva, 100m, xii.1992, P. Hanson, (UWY); ♀, Heredia, 3km S. Puerto Viejo OTS, La Selva, 100m. 1–15.ix.1992, P. Hanson, huertos, set de trampas malaise de G. Wright (UCR); ♀, La Selva, 15.xii.1993, J Longino (M/04/272) (UK); 2♀, Heredia, Est. Biol. La Selva. 50–150m, 10° 26'N 84° 01'W, x.1992, P. Hanson, C Godoy (UCR) (UCOB); ♀, Limón. 16km W. Guápiles, 400m, i–iv. 1992, col. Paul Hanson (UCR).

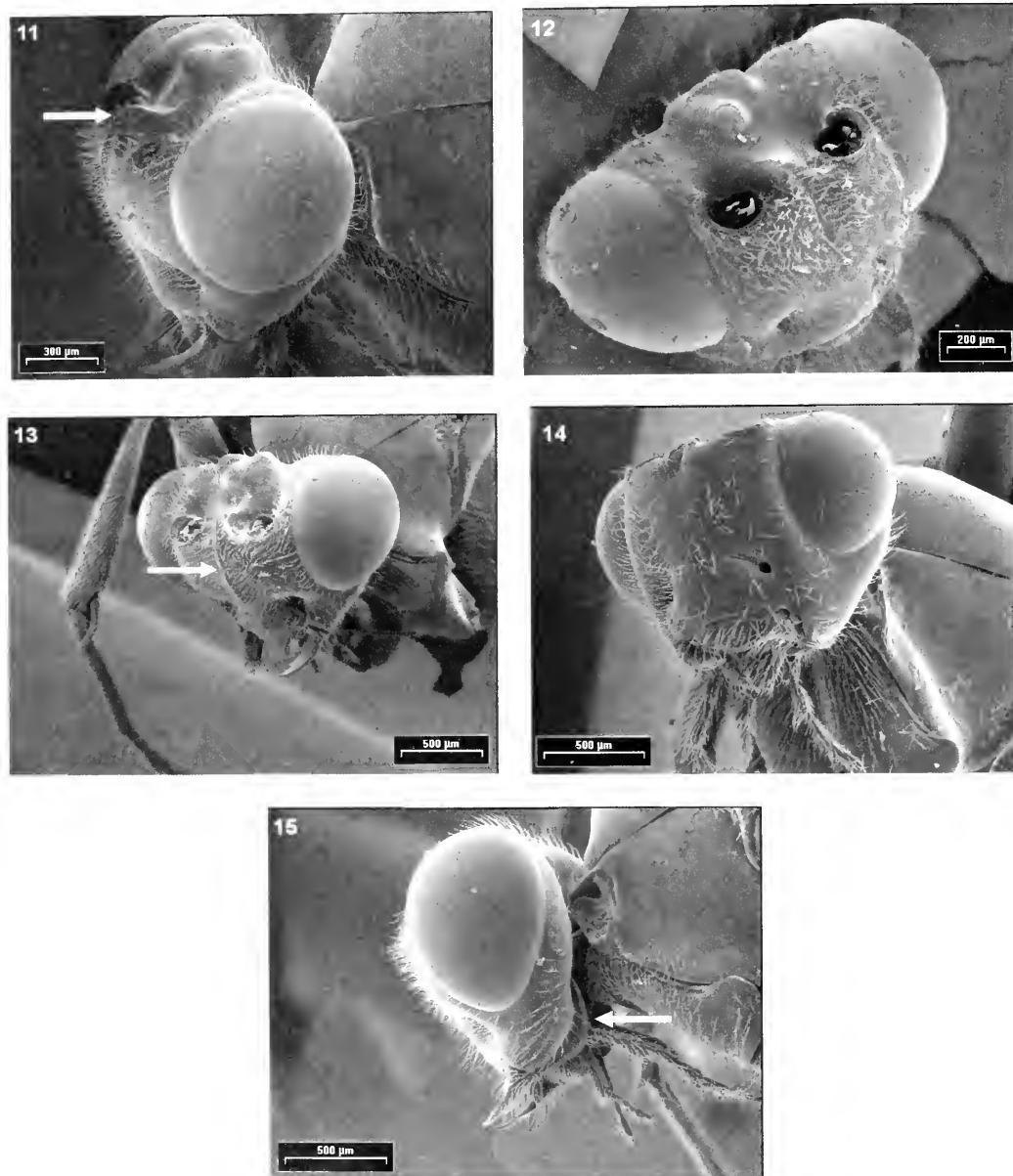
**Distribution.**—Known only from lowland Atlantic rain forests in Costa Rica, up to 900m.

**Etymology.**—From Greek *acrolophus* that means keel, in reference to the longitudinal carina on the face in this species.

***Sesioctonus amazonensis* Briceño, sp. n.**

**Diagnosis.**—*S. amazonensis* share characters with *S. armando* from which it is separated by the lack of longitudinal rugosities on the median areola of metanotum and the presence of a complete epicnemial carina.

**Description.**—♀. *Length.* Body 5–7 mm (7.0). **Head:** Flagellum with 35–38 flagellomeres (38). Interantennal space with rounded longitudinal keel. Antennal sockets moderately excavated. Face without median longitudinal carina. Genae not ex-



Figs. 11-15. Head. 11, *S. acrolophus*, arrow shows interantennal space with a sharp longitudinal keel. 12, *S. dichromus* in dorsal view showing interantennal space with a rounded longitudinal keel or absent. 13, *S. acrolophus*, arrow shows face with median longitudinal carina. 14, *S. brasiliensis*. 15, *S. acrolophus*, arrow shows expanded gena.

panded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible flat, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial pal-

pomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal

carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina, sharp, complete, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 5–9 spines (9). Hind tibia with 10 spines. Hind femur 3.51 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 4–5 hamuli (5). **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.01. Ovipositor 7 mm. **Color:** Head melanic. Antenna melanic. Maxillary palpomeres yellowish orange except basal two palpomeres melanic. Labial palpomeres yellowish orange. Mesosoma yellowish orange. Forelegs yellowish orange except femur sometimes melanic ventrally. Midlegs yellowish orange except tibia and tarsus melanic. Hindleg melanic with coxa yellowish orange. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing banded from base, yellow, infuscate, yellow, infuscate. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—*Holotype*. ♀. Brasil: Amazonas, Res. Ducke, 26km NE Manaus, 22.07.1981, J.A. Rafael, trampa malaise (CNC). **Paratypes.** BRASIL: ♀, same data as holotype (CNC); ♀, Manaus, ZF3, Km 23, Faz. Esteio, Res 1112; B. Klein col. 21.1.1986 (INPA).

**Distribution.**—This species is known only from the Amazonas region of Brasil.

**Etymology.**—This species is named after the locality of the holotype specimen.

#### *Sesioctonus ammosakron* Briceño, sp. n.

**Diagnosis.**—Epicnemial carina absent, a characteristic shared with *S. chrestos* and *S. grandis*. However, fore tibial with spines

are present the longitudinal carina of the median metasomal tergite are absent in *S. chrestos*. *S. grandis* can be separated by its larger size and the presence of 4 maxillary palpomeres.

**Description.**—♀. **Length.** Body 3.5 mm.

**Head:** Flagellum with 24 flagellomeres. Interantennal space without longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 5 palpomeres. Third and fourth labial palpomeres not fused. **Mesosoma:** Subpronope oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina completely absent. Foretibial spines absent. Midtibia with 9 spines. Hind tibia with 15 spines. Hind femur 3.14 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 3 hamuli. **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.32. Ovipositor 3.5 mm. **Color:** Head yellowish orange except vertex and occiput melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma yellowish orange sometimes melanic. Forelegs yellowish orange. Midlegs yellowish orange. Hindleg yellowish orange except tibia and tarsus melanic distally. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange but third tergum with median tergite melanic in posterior quarter; fourth tergum with median tergite melanic and

fifth to eighth metasomal terga mostly yellowish orange but median tergites melanic centrally. Ovipositor yellowish orange.

♂.—Unknown.

*Material examined.*—*Holotype*. Costa Rica: ♀, Puntarenas, San Vito, Est. Biol. Las Alturas, 1500m. iii.1992, Paul Hanson. (UWY).

*Distribution.*—This species is known only from the Puntarenas region of Costa Rica.

*Etymology.*—From Greek *ammos* that means sand and *akron* that means top, in reference to holotype locality, Puntarenas.

#### *Sesioctonus analogus* Briceño, sp. n.

*Diagnosis.*—*S. analogus* can be distinguished from most *Sesioctonus* species by the presence of 5 maxillary palpomeres and 4 labial palpomeres. However, this character occurs in 5 other species of the genus, of which *S. acrolophus* is closest to *S. analogus*. These two species are separated by the presence of a longitudinal carina on the face of *S. acrolophus*, which is absent in *S. analogus*.

*Description.*—♀. *Length*. Body 10 mm. *Head*: Flagellum with broken after flagellomere 20. Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae strongly expanded posteroventrally. Occipital tubercles present. Occiput excavated. Maxilla with 5 palpomeres. Third and fourth labial palpomeres not fused. *Mesosoma*: Subpronope oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina present. Epicnemial carina blunt, incomplete dorsally, straight medially (between forecoxae). Foretibial spines present. Midtibia with 18 spines. Hind tibia with 21 spines. Hind femur 2.88 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of fore-

wing present. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 4 hamuli. *Metasoma*: Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.99. Ovipositor 8 mm. *Color*: Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma yellowish orange. Forelegs melanic sometimes coxa and tarsus yellowish orange. Midlegs melanic sometimes coxa, femur and basitarsus yellowish orange. Hindleg melanic, sometimes coxa, femur and basitarsus yellowish orange basally. Forewing yellow basally and infuscate apically. Stigma melanic. Hind wing yellow basally infuscate apically. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

*Material examined.*—*Holotype*: Costa Rica: ♀, Est. Pitilla, 9km S, Sta. Cecilia, A.C., Guanacaste, Prov. Guana, 700m, v.1994, P. Ríos, Malaise (INBio).

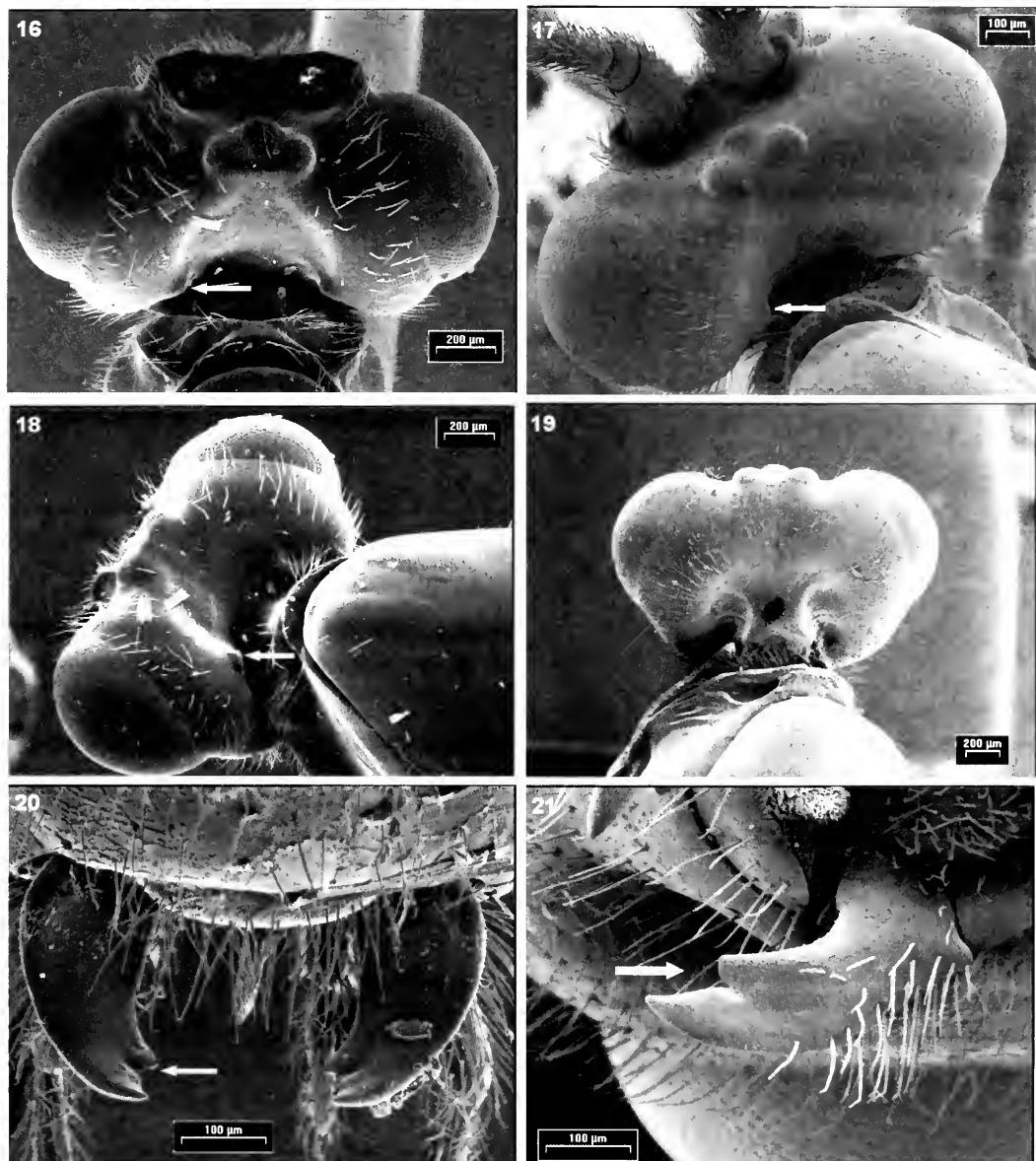
*Distribution.*—This species is known only from lowlands of Costa Rica up to 700m.

*Etymology.*—This species name refers to a similarity with *S. acrolophus*.

#### *Sesioctonus areolatus* Briceño, sp. n.

*Diagnosis.*—Presence of central areola on the propodeum, median longitudinal carina of the scutellar depression, foretibial with spines and epicnemial carina complete and straight medially. Also, the body size is small.

*Description.*—♀. *Length*. Body, 4–5 mm (4.2). *Head*: Flagellum with 26–28 flagellomeres (26). Interantennal space without longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave, outer tooth of mandible not longer than



Figs. 16–21. Head. 16–19, Occipital tubercles. 16, 18, *S. dichromus*. 17, *S. diazi*. 19, *S. grandis* without tubercles. 20–21, Mandible teeth. 20, *S. dichromus* with outer tooth not longer than inner tooth. 21, *S. acrolophus* with outer tooth longer than inner tooth.

inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression present. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and

with lateral carinae present and meeting posteriorly. Propodeum flat, median longitudinal carina present. Epicnemial carina sharp, complete, straight medially (between forecoxae), sometimes bilobed. Foretibial spines present. Midtibia with 7–8 spines (7). Hind tibia with 10–12 spines

(10). Hind femur 3.35 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing present. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 3 hamuli. **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.04. Ovipositor 3–4.3 mm (4.0). **Color:** Head yellowish orange. Antenna melanic. Maxillary and labial palpomeres yellowish orange, sometimes melanic. Mesosoma entirely yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange sometimes tibia melanic. Hindleg yellowish orange with tibia yellowish orange but melanic distally; and tarsus melanic, or yellowish orange. Forewing entirely infuscate or infuscate with hyaline spots. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—*Holotype*. Costa Rica: ♀, Puntarenas, San Vito, Est. Biol. Las Alturas, 2100m, iii–v.1995, Paul Hanson (UWY). *Paratypes*. Costa Rica: 3♀, Puntarenas, San Vito, Est. Biol. Las Alturas, 1500–2100m, v.1992, iii–v.1995, Paul Hanson (UWY); ♀, Guanacaste Prov., 300m, deciduous woods (25–30 yrs), 4.ix–5.x.1985, Gauld & Janzen (UK). Honduras: ♀, Cortés, Parque Nacional Cusuco 5km N de Buenos Aires, 15°29'N 88°13'W, 15.x.1995, malaise trap, R. Cave (MZLU).

**Distribution.**—This species is known only from Costa Rica and Honduras.

**Etymology.**—From Latin *areolatus* that means areolated, in reference to the central areola on the propodeum in this species.

#### *Sesiocionus ariasi* Briceño, sp. n.

**Diagnosis.**—*S. ariasi* can be distinguished from the rest of *Sesiocionus* species by the following combination of char-

acters: presence of occipital tubercles, median areola of metanotum with lateral carinae not meeting posteriorly, and presence of the longitudinal carinae in the propodeum. This combination could confuse *S. ariasi* with *S. acrolophus*, however these species can be separate easily because the number of maxillary and labial palpomeres is fewer in *S. ariasi*.

**Description.**—♀. **Length.** Body, 6–8.5 mm (8.0). **Head:** Flagellum with 30–34 flagellomeres (33). Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope oval. Longitudinal carina of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum convex, median longitudinal carina present. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 8 spines. Hind tibia with 14–16 spines (15). Hind femur 3.32 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing present. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 5 hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.18. Ovipositor 5–8 mm (7.5). **Color:** Head melanic. Antenna melanic. Maxillary palpomeres melanic, sometimes yellowish orange except basal two palpomeres melanic. Labial palpomeres melanic. Mesosoma mostly yellowish orange with pronotum melanic anteriorly, propleuron and meta-

pleuron melanic, or yellowish orange, sometimes melanic posteriorly. Forelegs melanic except tibia melanic, or yellowish orange and tarsus yellowish orange. Midlegs melanic except tarsus with basitarsus sometimes yellowish orange in basal half. Hindleg melanic. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma mostly yellowish orange except fifth to eighth metasomal terga melanic. Ovipositor yellowish orange except apical eighth melanic.

♂.—Essentially as female.

*Material examined.*—*Holotype*: Brazil: ♀, Matogrosso, 12° 31' S, 55° 37' W, ii. 1976, M. Alvarenga (CNC). *Paratypes*: Colombia: ♂, Cundinamarca, Monterredondo, 14.xii.1958, J. Foerster (CNC), ♀, Antioquia, Mun. San Luis R.N. Rio Claro, El Refugio 5° 47'N, 75° 0'W, 500m, malaise, 13.i.98. Diego Campos (UK); ♀, Amazonas, PNN. Amacayacu, Mocagua, 3° 23'S, 70° 06'W, 150m, malaise, 26.ii-12.iii.2001, B. Amado (UK); ♀, Cauca, PNN. Gorgona, Mancora, 2° 58' N, 78° 11' W, 60m, malaise, 26.vi-18.vii.2000, H. Torres (UK). Costa Rica: ♂, Est. Hitoy Cerere, 100m, R. Cerere, Res. Biol. Hitoy Cerere, Prov. Limón, vii.1992, G. Carballo (INBio). Bolivia: ♀, Staudinger K (ZSBS); Ecuador: ♂, Napo, Prov. Sacha, 9.iii.1983, L. Huggert (CNC).

*Distribution.*—From Costa Rica in Central America to Brazil, Bolivia and Colombia in South America.

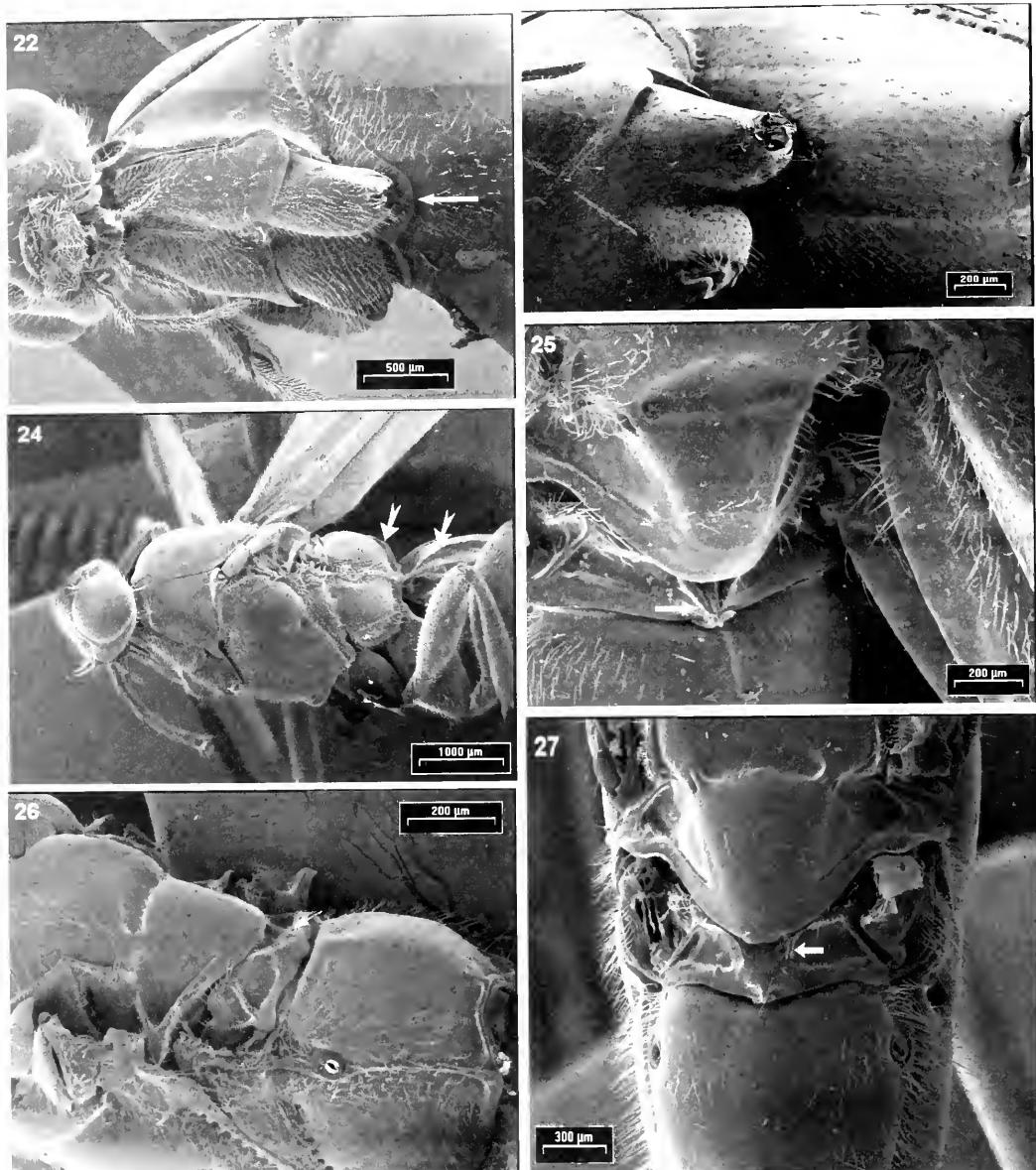
*Etymology.*—This species is named in honor of Quintín Arias, for his friendship and advise regarding computer software.

### *Sesioctonus armandoi* Briceño, sp. n.

*Diagnosis.*—*S. armandoi* can be distinguished from the rest of *Sesioctonus* species by the following combination of characters: occipital tubercles absent, epicnemial carina incomplete laterally, median areola of metanotum with longitudinal rugosities and with lateral carinae meeting posteriorly. This combination is present in *S. galeos* but the epicnemial carina in this

latter species is straight and not bilobed as *S. armandoi*.

*Description.*—♀. *Length.* Body, 6 mm. *Head*: Flagellum with 34 flagellomeres. Interantennal space with rounded longitudinal keel. Antennal sockets moderately excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. *Mesosoma*: Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum with longitudinal rugosities; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina, sharp, incomplete dorsally, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 5 spines. Hind tibia with 10 spines. Hind femur 3.27 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 4 hamuli. *Metasoma*: Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.94. Ovipositor 6 mm. *Color*: Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma melanic except metanotum, propodeum and metapleuron yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange. Hindleg melanic except trochanter and trocantellus yellowish orange. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing banded from base, yellow, infuscate, yellow, infuscate. Metasoma yellowish orange until third tergum, rest melanic. Ovipositor yellowish orange.



Figs. 22–27. 22–23, Epicnemial carina. 22, Complete and bilobed in *S. brasiliensis*, 23, incomplete and straight in *S. acrolophus*. 24, *S. acrolophus* in lateral view, right arrow shows longitudinal carina of propodeum and left arrow first metasomal segment with pair of lateral longitudinal carinae. 25–27, Median areola of metanotum. 25, Smooth with longitudinal carinae and lateral carinae meeting posteriorly in *S. acrolophus*. 26, Smooth with lateral carinae meeting posteriorly in *S. clavijoi*. 27, Smooth with lateral carinae not meeting posteriorly in *S. brasiliensis*.

♂.—Essentially as female.

*Material examined*.—*Holotype*: Ecuador: ♀, Napo & Coca Rivers, 2–10.v.1965, Luis Peña (AEI). *Paratypes*: Colombia: ♀, Amazonas, PNN Amacayacu Matamata, 8–12.iii.2000, Sharkey (UK).

N, 70° 06' W, 150m, 7–19.vii.2000, A Pariente (UK); ♂, Amazonas, PNN Amacayacu Mocagua, 3° 23'

*Distribution*.—This species is known only from Ecuador and Colombia.

**Etymology.**—This species is named in honor of Armando Briceño, Venezuelan entomologist, and my uncle.

***Sesiocrotus biospleres* Briceño, sp. n.**

**Diagnosis.**—*S. biospleres* can be distinguished by the following combination of characters: genae expanded posteriorly, occipital tubercles absent, epicnemial carina incomplete laterally, foretibia with spines and median tergite of first metasomal tergum with pair of longitudinal carinae.

**Description.**—♀. Length. Body, 6–8 mm (6.5). **Head:** Flagellum with 30–35 flagellomeres (34). Interantennal space with rounded longitudinal keel, or keel lacking. Antennal sockets not excavated. Face without median longitudinal carina. Genae expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina present. Epicnemial carina, sharp, incomplete laterally, bilobed medially (between forecoxae). Foretibial spines present. Midtibia with 6–10 spines (9). Hind tibia with 10–14 spines (14). Hind femur 3.11 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 3 hamuli. **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.98. Ovipositor 5.5–6.5 mm (6.3). **Color:** Head yellowish orange. Antenna melanic. Maxillary and

labial palpomeres yellowish orange. Mesosoma yellowish orange. Forelegs yellowish orange except femur and tibia melanic, or melanic with yellowish orange apically. Midlegs yellowish orange except tibia melanic apically. Hindleg yellowish orange except tibia yellowish orange with apical third melanic and tarsus melanic with basitarsus yellowish orange in basal third. Forewing yellow basally and infuscate apically. Stigma melanic. Hind wing yellow basally infuscate apically. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—**Holotype:** Costa Rica: ♀, Prov. Puntarenas, Est. Agujas, Río Agujas, sendero Samia, 300m, 1–3.vi.1997, A. Azofeifa (INBio). **Paratypes:** Costa Rica: ♀, Rancho Quemado, 200m, Peninsula de Osa, Prov. Puntarenas, vi.1992, F. Quesada y M. Segura (INBio); ♀, Rancho Quemado, Peninsula de Osa, Prov. Puntarenas, 200m, 01.xi–01.xii.1992, A. L. Marín (INBio). Panama: ♀, Barro Colorado Is, 9°9'N 79°51'W, 11–18.v.1994, J. Pickering (UK).

**Distribution.**—This species is known only from lowlands of Prov. Puntarenas, Costa Rica and Barro Colorado in Panama.

**Etymology.**—From Greek *bios* meaning life and *pleres* that means abundance.

***Sesiocrotus boliviensis* Briceño, sp. n.**

**Diagnosis.**—*S. boliviensis* can be separated by the following combination of characters: interantennal space with a longitudinal rounded keel and the presence of the occipital tubercles.

**Description.**—♀. Length. Body, 10 mm. **Head:** Interantennal space with rounded longitudinal keel. Antennal sockets moderately excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Third and fourth labial palpomeres completely fused. **Mesosoma:**

Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 6 spines. Hind tibia with 19 spines. Hind femur 3.21 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 5 hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.79. Ovipositor 10 mm. **Color:** Head melanic except labial palpomeres melanic. Antenna melanic. Mesosoma yellowish orange sometimes pronotum and propleuron melanic. Forelegs melanic. Midlegs melanic. Hindleg melanic. Forewing banded from base infuscate, yellow, infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—Holotype. Bolivia: ♀, Staudinger K (ZSBS).

**Distribution.**—This species is known only from Bolivia, South America.

**Etymology.**—The name *boliviensis* refers to the country of origin of the holotype.

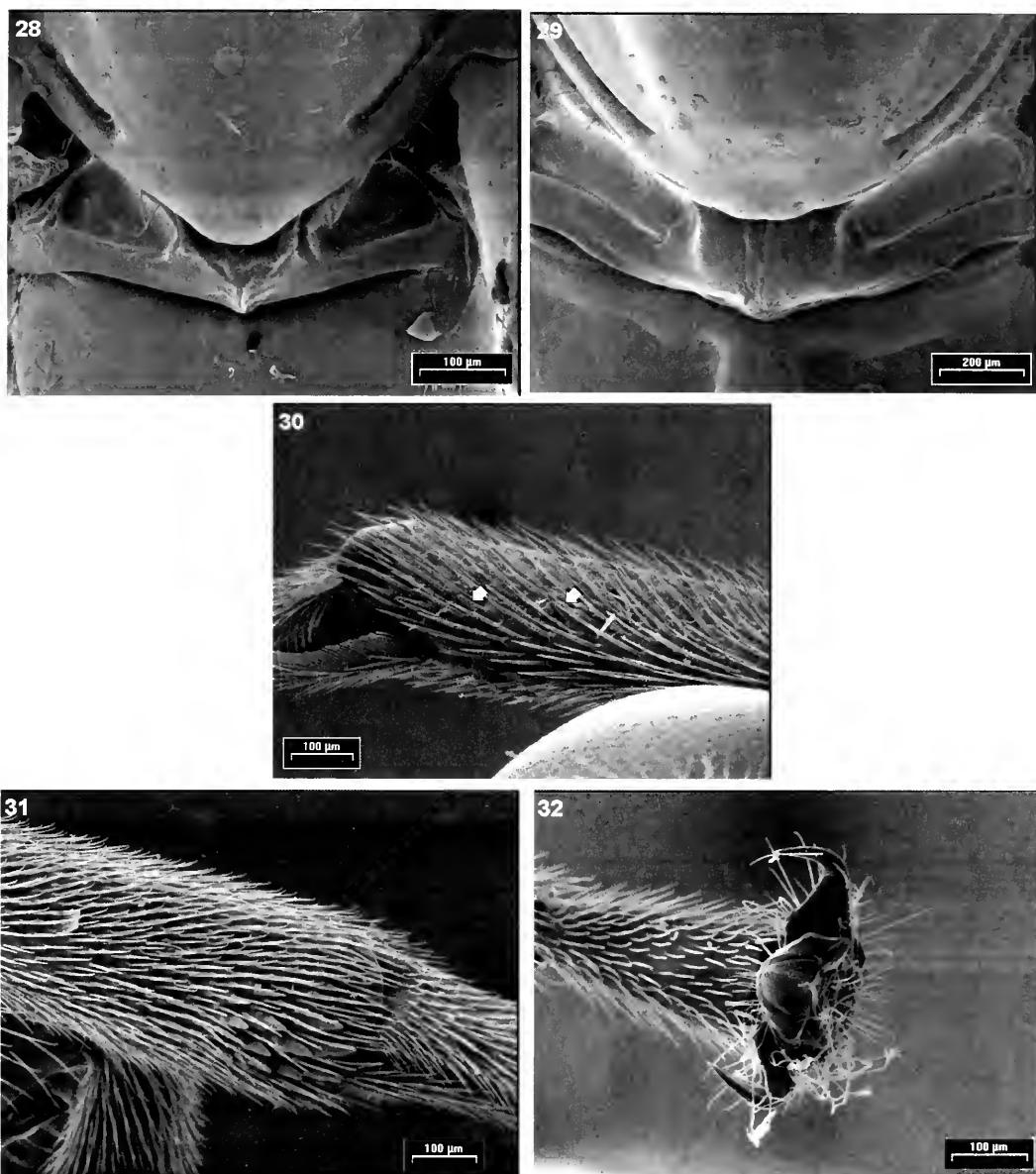
#### *Sesioctonus brasiliensis* Briceño, sp. n.

Figs. 14, 22, 27, 34

**Diagnosis.**—*S. brasiliensis* is the only species with metasoma reddish brown and forewing with a large hyaline spot. Also, the median areola of metanotum does not have longitudinal and lateral carinae, nor longitudinal rugosities. Occipital tubercles are present in this species.

**Description.**—♀. **Length.** Body, 9–10 mm

(9.0). **Head:** Flagellum with 30–35 flagellomeres (33). Interantennal space with rounded longitudinal keel. Antennal sockets deeply excavated, sometimes moderately excavated. Face without median longitudinal carina. Genae moderately expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and lacking lateral carinae. Propodeum convex, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 8–11 spines (8). Hind tibia with 14–17 spines (14). Hind femur 3.64 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing present. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 5–6 hamuli (6). **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.09. Ovipositor 8 mm. **Color:** Head melanic. Antenna melanic. Maxillary palpomeres yellowish orange. Labial palpomeres melanic. Mesosoma melanic. Forelegs mostly yellowish orange except coxae melanic, tibia yellowish orange, or melanic; and tarsus mostly yellowish orange, but apical tarsomere melanic. Midlegs mostly melanic except trochanter and trocantellus yellowish orange, femur yellowish orange in basal half, melanic apically. Hindlegs mostly melanic except trochantellus melanic, or yellowish orange. Forewing infuscate with large hyaline spot. Stigma melanic. Hind wing entirely infuscate. Metasoma reddish brown with the last



Figs. 28–32. Median areola of metanotum. 28, Smooth with lateral carinae not meeting posteriorly in *S. diazi*. 29, With longitudinal rugosities and lacking lateral carinae in *S. grandis*. 30–32, 30, Foretibia of *S. acrolophus* showing spines. 31, Midtibia of *S. dichromus* showing spines. 32, Simple tarsal claws in *S. acrolophus*.

four segments melanic. Ovipositor yellowish orange.

♂.—Essentially as the female.

*Material examined.*—*Holotype*. Brazil: ♀, Nova Teutonia, 27°11'S 52°23'W, 300–500m, 24.i.1939, Fritz Plaumann (CNC). *Paratypes*. Brazil: ♀, Nova Teutonia,

27°11'S 52°23'W, 300–500m, Fritz Plaumann; 2♀, same data except 30.i.1939, 26.i.1939 (BMNH); ♀, same data except vii.1940; ♂, same data except 18.v.1954 (AEI); 5♀, same data except ii.1967, iii.1965, xi.1968, ii.1966; ♂, same data except 21.x.1940 (CNC); 2♀, same data ex-

cept 6–10.iii.1967 (UK); ♀, Represa Río Grande, Guanabara, xii.1967. M. Alvarenga (AEI).

*Distribution.*—This species is known only from Nova Teutonia region of Brazil.

*Etymology.*—This species is named after the country of the holotype specimen.

*Sesioctonus chaconi* Briceño, sp. n.

*Diagnosis.*—This species may be recognized by the combination of a long outer tooth of the mandible and the absent of the 3RSa vein in the forewing.

*Description.*—♀. Length. Body, 6–9 mm (6.5). **Head:** Flagellum with 29–33 flagellomeres (29). Interantennal space with rounded longitudinal keel. Antennal sockets moderately excavated, or not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina, sharp, complete, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 8–13 spines (9). Hind tibia with 13–16 spines (15). Hind femur 3.39 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 4–5 hamuli (4). **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.19. Ovipositor 6–8 mm (6.1). **Color:** Head melanic except maxillary palpomeres yellowish or-

ange. Antenna melanic. Mesosoma mostly yellowish orange except pronotum melanic anteriorly; metanotum, propodeum and metapleuron yellowish orange or melanic; and propleuron always melanic. Forelegs with coxa, trochanter and trocantellus melanic, or yellowish orange; femur yellowish orange, melanic basally; tibia and tarsus yellowish orange. Midlegs with coxa yellowish orange ventrally, melanic dorsally; trochanter melanic, trochantellus yellowish orange, femur melanic in basal half, yellowish orange apically, or yellowish orange, tibia yellowish orange, or melanic, and tarsus yellowish orange but apical tarsomere melanic. Hindleg melanic except coxa yellowish orange in basal half, melanic apically; femur melanic, or yellowish orange, melanic basally. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing banded from base, yellow, infuscate, yellow, infuscate. Metasoma yellowish orange except first metasomal tergum yellowish orange, but median tergite melanic centrally and fifth to eighth metasomal terga melanic. Ovipositor yellowish orange.

♂. Essentially as female.

*Material examined.*—**Holotype.** Ecuador: ♀, Napo, Tena, 23.v.1977, DL& SS Vincent (CNC). **Paratypes.** Ecuador: ♀, Banos, 700m, 20.iii.1939, W. Clarke-MacIntyre (AEI); ♀, Coca, v.1965, Luis Peña (AEI); ♀, Prov. Santa Clara, 30.vi.1976, P. M. Turner (CNC). Peru: ♂, Yahuar Mayo, 8.ii.1910, CHTTownsend col (CNC); ♀, Loreto, Pucallpa, 12.vi.1951, J. M. Schuncke (CNC); ♀, Loreto, Boquerón Abad, 27.xii.1961, J. M. Shuncke (CNC); ♀, Avispas, 30m nr. Marcapata, 1–15.x.1962, Luis Peña (AEI); ♀, Loreto, Boquerón, 500m, 7–14.vii.1965, J. Schuncke (UK). Colombia: ♀, Putumayo, Villa Garzón, 8mi. s. Mocoa, 3.viii.1978, M. Cooper (CNC).

*Distribution.*—This species is distributed in northwestern of South America, from Colombia to Peru and Ecuador.

*Etymology.*—This species is named in

honor of Mr. Aníbal Chacón, who during many years has shared with Venezuelan entomologists his passion for entomology and insects collecting in Venezuela.

*Sesioctonus chrestos* Briceño, sp. n.

**Diagnosis.**—*S. chrestos* is known only from one male specimen, however can be distinguished from all other species by the following combination of characters: maxilla with 5 palpomeres, labium with 4, epicnemial carina absent and foretibia with spines.

**Description.**—♂. Length. Body, 5.5 mm. **Head:** Flagellum with broken after flagellomere 12. Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Maxilla with 5 palpomeres. Third and fourth labial palpomeres partly fused. **Mesosoma:** Subpronope oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina completely absent. Foretibial spines present. Midtibia with 2 spines. Hind tibia with 5 spines. Hind femur 3.06 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSA vein of forewing present. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 3 hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.04. **Color:** Head yellowish orange. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma yellowish orange except scutellum, metanotum, propodeum, mesopleuron and metapleuron melanic. Forelegs yellowish

orange. Midlegs mostly melanic except femur yellowish orange apically; and tibia yellowish orange. Hindleg melanic. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma with first and second terga yellowish orange, but median tergite melanic centrally; rest of metasomal terga melanic.

♀.—Unknown.

**Material examined.**—Holotype. Peru: ♂, Marcapata (TMB).

**Distribution.**—This species is known only from Peru.

**Etymology.**—From Greek *chrestos* that means good, useful.

*Sesioctonus clavijoi* Briceño, sp. n.

Fig. 26

**Diagnosis.**—*S. clavijoi* shows color patterns similar to *S. areolatus*, however can be separated from the latter by the presence of the bilobed epicnemial carina. *S. areolatus* has this carina straight and also has a central areola on the propodeum and a longitudinal carina on the scutellar depression, both of which are absent in *S. clavijoi*.

**Description.**—♀. Length. Body, 4–5.5 mm (5.1). **Head:** Flagellum with 25 flagellomeres. Interantennal space lacking longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Longitudinal carinae of scutellar depression absent. Scutellum flat. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibial spines present. Midtibia with 5–9 spines (8). Hind tibia with 10–12 spines (12). Hind femur

3.1 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing absent. 2-1A vein of hind wing not tubular. CUb vein of hind wing not tubular. Hind wing with 3 hamuli. **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.04. Ovipositor 4 mm. **Color:** Head yellowish orange. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange. Hindleg yellowish orange except tibia mostly yellowish orange, but melanic apically and tarsus melanic, or melanic with basitarsus yellowish orange basally, or melanic with basitarsus yellowish orange in basal third. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Essentially as female.

**Material examined.**—**Holotype.** Costa Rica: ♀, Puntarenas, Golfo Dulce, 24km W. Piedras Blancas, 200m, iv.1993, Paul Hanson (UWY). **Paratypes.** Costa Rica: 3♀, same data as holotype, except 10–200m, xii.1992, ii.1993, Paul Hanson (UWY); ♂, Puntarenas, San Vito, Est. Biol. Las Alturas, 1500m, iii.1992, Paul Hanson (UWY). Peru: ♀, Quincemil, 750m nr. Marcapata, 10–15.xi.1962, Luis Peña (AEI). Mexico: ♀, Vista Hermosa, Oaxaca, 96.5km SW Tuxtepec, 19.x.1962, H. & M. Townes (AEI).

**Distribution.**—Southern Mexico, Costa Rica and Peru.

**Etymology.**—This species is named in honor of José Clavijo A., venezuelan taxonomist, my professor and my friend, who has shared with me many of my entomologist dreams and has been an important part of my life. Thanks for all that you have done for me.

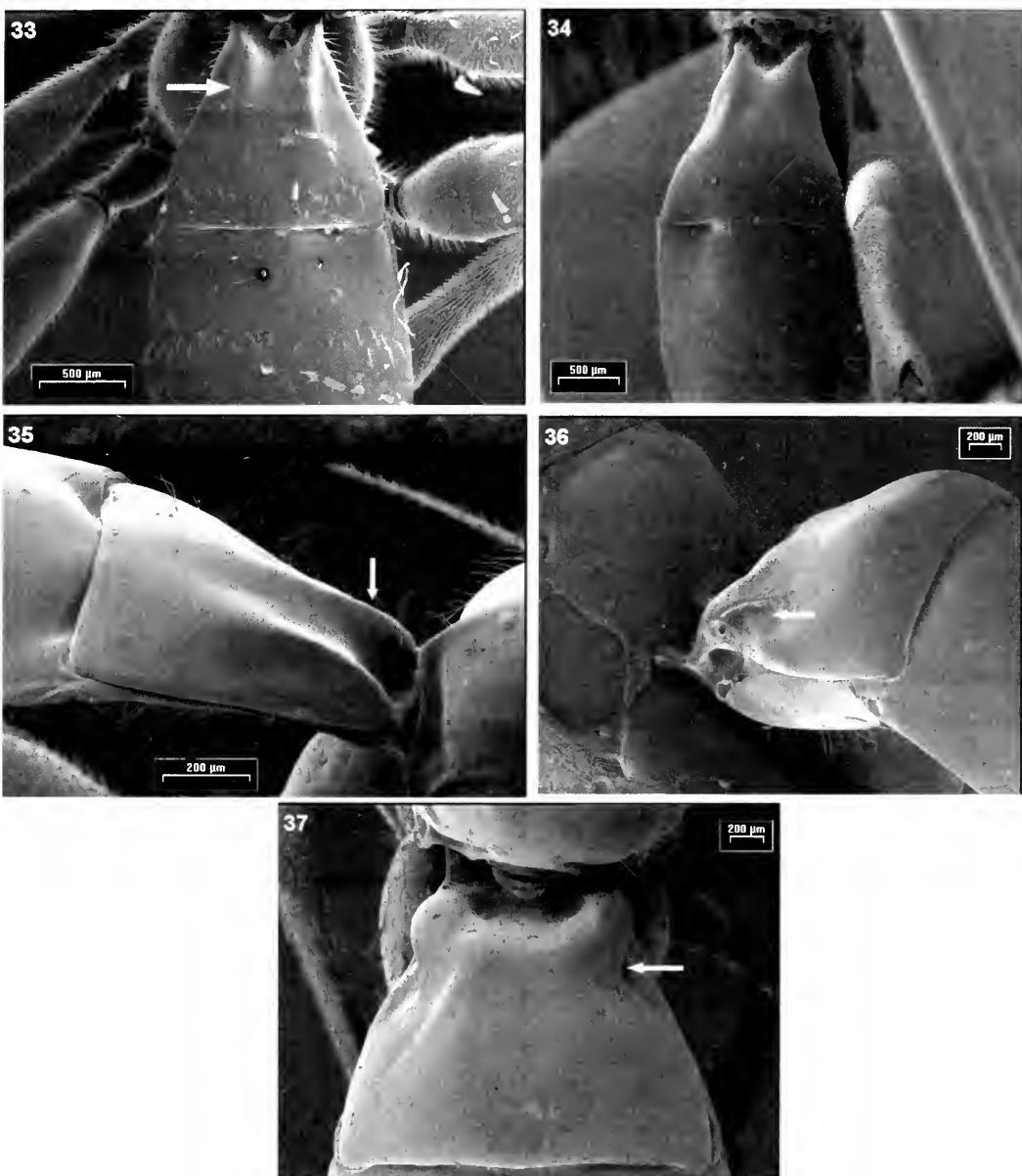
*Sesioctonus diazi* Briceño, sp. n.

Figs. 17, 28

**Diagnosis.**—*S. diazi* is not an easy species to distinguish because of intraspecific

variation, especially in color pattern. It can be confused with specimens of *S. chaconii*, and separation of these species is complicated because the differences are primarily in the relative sizes of the mandible teeth.

**Description.**—♀. **Length.** Body, 7–8 mm (7.5). **Head:** Flagellum with 28–34 flagellomeres (33). Interantennal space with rounded longitudinal keel. Antennal sockets moderately excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular or oval-shape. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina, sharp, complete, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 8–11 spines (10). Hind tibia with 15–23 spines (17). Hind femur 3.01–3.22 (3.08) times as long as wide. (RS+M)a vein of forewing complete or incomplete. 3RSa vein of forewing present. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 4–5 (5) hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.84–1.03 (0.84). Ovipositor 5–8 mm (7.1). **Color:** Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange except basal two palpomeres melanic. Mesosoma mostly yellowish orange sometimes pronotum and propleuron melanic. Forelegs melanic, or tarsus mostly yellowish orange, but apical tarsomere melanic. Midlegs variable, tarsus melanic, or yellowish orange



Figs. 33–37. First metasomal tergite. 33,35, With lateral longitudinal carinae. 33, *S. dichromus*. 35, *S. acrolophus*. 34, *S. brasiliensis* without lateral longitudinal carinae. 36–37, *S. grandis* showing depression posterad spiracle.

but apical tarsomere melanic. Hindlegs melanic but coxa can be yellowish orange in basal half, melanic apically, or yellowish orange with melanic spots laterally, or melanic, or yellowish orange basally, otherwise melanic. Forewing yellow basally and infuscate apically, or banded from

base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing yellow basally infuscate apically. Metasoma yellowish orange. Ovipositor yellowish orange, or yellowish orange except apical eighth melanic.

♂.—The color pattern in males is essen-

tially as females except fifth to eighth metasomal tergite which sometimes can be yellowish orange with central portion of median tergite melanic.

*Material examined.*—*Holotype.* Costa Rica: ♀, Heredia, Est. Biol. La Selva, 50–150m, 10°26'N 84°01'W, viii.1998 (INBio). *Paratypes.* Costa Rica: ♀, Nara NE Quepos, 16.vii.1975, W.J.Hanson (CNC); ♀, Prov. Alajuela, 28.v.1972, J.F.Alvarez (UCR); ♂, Alajuela, Upala, Colonia Libertad, 450m, 1–6.v.1988, González & Soto (UCR); ♀, Prov. Golfo Dulce, 24km W Pan-Am highway, 200m, iii–v.1989, Gauld (BMNH); 3♀, 2♂, same data as holotype except, 02.v.1993, vi.1993, vii.1993, 03.viii.1993, v.1996 (INBio)(UCOB)(UK); ♀, Prov. Puntarenas, Est. Agujas, sendero Ajo., 300m, 14–24.viii.1996, A. Azofeifa (INBio). Guatemala: ♀, Concepción, 1400m (UK). Panama: 4♀, Barro Colorado Is, 9°9'N 79°51'W, v.1939, Jas Zetek (USNM), 5–12.v.1993, 23–30.iii.1994, 30.iii–6.iv.1994. J. Pickering (UK); 1♀, 1♂, Portobello, 24.ii.1911, 13.iii.1911, A. Busk (CNC); ♀, San Blas Nusagandi Reserve, 9°20'N 79°0'W, 20–27.xi.1993. J. Pickering (UK).

*Distribution.*—*Sesiocionus diazi* is distributed from Guatemala to Panama in Central America.

*Etymology.*—This species is named in honor of Francisco Díaz, venezuelan entomologist, for his contribution to the knowledge of Venezuela ichneumonids.

#### *Sesiocionus dichromus* Briceño, sp. n.

Figs. 12, 16, 18, 20, 31, 33

*Diagnosis.*—*S. dichromus* can be distinguished from other *Sesiocionus* species by the following combination of characters: occipital tubercles present, occiput excavated, median areola of metanotum with lateral carinae present and meeting posteriorly, the median tergite of first metasomal segment with well defined pair of lateral longitudinal carinae.

*Description.*—♀. *Length.* Body, 6–10 mm (9.5). *Head:* Flagellum with 30–35 flagellomeres (33). Interantennal space with

rounded longitudinal keel. Antennal sockets moderately excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. *Mesosoma:* Subpronope triangular or oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly, or lacking lateral carinae. Propodeum flat, median longitudinal carina present or absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibia spines absent. Midtibia with 7–13 spines (12). Hind tibia with 18–25 spines (19). Hind femur 3.28–3.6 times as long as wide (3.54). (RS+M)a vein of forewing complete or incomplete. 3RSA vein of forewing present or absent. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 5–7 hamuli (7). *Metasoma:* Median tergite of first metasomal segment with pair of lateral longitudinal carinae. Median tergite of first metasomal segment without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.97. Ovipositor 6–9 mm (9.0). *Color:* Head melanic including maxillary and labial palpomeres. Antenna melanic. Mesosoma melanic. Forelegs melanic. Midlegs melanic. Hindleg melanic. Forewing entirely infuscate, or hyaline basally, infuscate apically. Stigma melanic. Hind wing entirely infuscate, or infuscate with large hyaline spots, or hyaline basally, infuscate apically. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Essentially as the female.

*Material examined.*—*Holotype.* Costa Rica: ♀, Alajuela, San Ramón, 800m, 29.i–03.ii.1995, G. Carballo (INBio). *Paratypes.* Costa Rica: 29♀, Heredia, Est. Biol. La Selva, 50–150m, 10°26'N 84°01'W, 11–

17.vi.1986, 2.v.1993, vi.1993, viii.1993, ix.1993, 01.ix.1993, 16.ix.1993, xii.1993, 22.iii.1994, 29.ix.1995, ix.1995, 15.xii.1995, 14.xii.1995, ii.1996, 01.iii.1996, iii.1996, vi.1996, 2.v.1996, 15.v.1996, 02.x.1997, xi.1997, ix.1998, 22.i.1999 (INBio) (UK) (UCR) (UWY) (UCOB); ♂, Heredia, Est. El Ceibo, Braulio Carrillo, N.P. 400–600m, iii.1990, C. Chavez (INBio); 2♀, Est. Pitilla, 9km Sur Santa Cecilia, Guanacaste, 700m, xi.1988, C. Chavez & M. Espinoza, ii.1990, P. Ríos, C. Moraga & R. Blanco (INBio); 4♀, El Limón, Sector Cerro Cocorí, Finca de E. Rojas, 150m, v.1991, 5.vii–12.viii. 1992, 11.i–12.ii.1993, Trampa malaise (INBio); ♀, El Limón, 16km W Guapiles, Parque Nacional Braulio Carrillo, 400m, iv–v.1989, Gauld (BMHN); ♀, Limón, P N Tortuguero, Est. 4-esquinas, 0m, vi–viii.1989, Solano col (UWY); ♀, Puntarenas, Rancho Quemado, Peninsula de Osa, 200m, iv.1992, L.Brenes (INBio); ♀, Alajuela, Penas Blancas, 700m, viii.1987, E. Cruz (CNC); ♀, Alajuela, Sector Colonia Palmareña, 9km SO de Bajo Rodríguez, 700m, ix.1996, G. Carballo (INBio); ♀, San José, P.N. Braulio Carrillo, 9.5km E túnel, 1000m, viii–ix.1989 (UWY); ♂, Alajuela, Sector San Ramón, 800m, 11–15.iv.1994, M. Zumbado (INBio); ♀, Est. Biol. La Selva, 30.vi.1995 (UK). Mexico: ♀, Chiapas, Muste, 440m near Huixtla. 1970. Mal. trap. Welling (CNC).

**Distribution.**—This species is known from México to Costa Rica.

**Etymology.**—From Greek *di* that means two and *chromos* that means color, in reference to the color pattern of the species, half melanic, half yellowish orange.

#### *Sesioctonus dominicus* Briceño, sp. n.

**Diagnosis.**—*S. dominicus* is known only from males specimens. However, it can be separated from all other *Sesioctonus* species by its small size (2.0–3.5mm) and totally hyaline wings.

**Description.**—♂. **Length.** Body, 2–3.5 mm (2.5). **Head:** Flagellum with 23–27 flagellomeres (25). Interantennal space lacking

longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible flat, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope elongate-oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina (difficult to see), sharp, incomplete dorsally, straight medially (between forecoxae). Foretibial spines absent. Midtibia with 7–10 spines (8). Hind tibia with 13–16 spines (15). Hind femur 1.14 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing absent. 2-1A vein of hind wing not tubular. CUB vein of hind wing not tubular. Hind wing with 3 hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.10. **Color:** Head black except face yellowish orange. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma melanic except propodeum, propleuron and metapleuron yellowish orange and pronotum yellowish orange, or melanic. Forelegs yellowish orange. Midlegs yellowish orange except tibia melanic, or yellowish orange. Hindleg yellowish orange except tibia melanic and tarsus melanic. Forewing hyaline. Stigma melanic. Hind wing hyaline. Metasoma with first and second terga yellowish orange, the rest melanic.

♀.—Unknown.

**Material examined.**—**Holotype.** Dominica W.I.: ♂, Springfield, xi.1967, N.L.H Krauss (UK). **Paratypes.** Dominica W.I: 2♂, Clarke

Hall, Layou Vall, 10–17.ii.1965, 20–28.ii.1965, H.E.Evans (UK) (USNM); ♂, Mth. Layou R, 13.iii.1965, H.E.Evans (USNM); ♂, Hillsborough, 15.iii.1965 (USNM).

**Distribution.**—This species is known only from the Dominica W. I. in the Caribbean.

**Etymology.**—This species is named after the locality of the holotype specimen.

*Sesioctonus eumenetes* Briceño, sp. n.

**Diagnosis.**—*S. eumenetes* is known only from one specimen, however, can be distinguished from all other *Sesioctonus* species by the following combination of characters: occipital tubercles absent, presence of median longitudinal carina on the propodeum, epicnemial carina complete, median areola of metanotum smooth and a pair of longitudinal carinae on the first metasomal tergite.

**Description.**—♀. *Length.* Body, 6 mm. **Head:** Flagellum broken after flagellomere 11. Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles absent. Occiput excavated. Mandible concave, outer tooth of mandible longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibia spines absent. Midtibia with 10 spines. Hind tibia with 15 spines. Hind femur 3.17 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing present. 2-1A vein of hind wing tubular. CUB vein of hind wing not tubular. Hind wing with 5 hamuli. **Metaso-**

**ma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.09. Ovipositor 6.5 mm. **Color:** Head melanic. Antenna melanic. Maxillary and labial palpomeres melanic. Mesosoma yellowish orange except pronotum mostly yellowish orange, melanic anteriorly and propleuron melanic. Forelegs melanic except coxa mostly yellowish orange and tarsus mostly yellowish orange, but apical tarsomere melanic. Middle legs melanic except coxa yellowish orange. Hindleg melanic except coxa yellowish orange and femur melanic in basal third, otherwise yellowish orange. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange. Ovipositor yellowish orange except apical eighth melanic.

♂.—Unknown.

**Material examined.**—*Holotype.* Costa Rica: ♀, San Vito Las Cruces, 1200m, 9.vii–7.viii.1982, B. Gill (CNC).

**Distribution.**—This species is known only from the Las Cruces region of Costa Rica.

**Etymology.**—From Greek *eumenetes* that means friend, in honor of my colleagues and friends Ana, Carmen Liceth, Carlos, Dorys and María del Carmen.

*Sesioctonus galeos* Briceño, sp. n.

**Diagnosis.**—*S. galeos* shows the following combination of characters: occipital tubercles absent, occiput not excavated, maxillary palpi with 4 palpomeres and labial palpi with 3, median areola of metanotum with longitudinal rugosities, epicnemial carina incomplete laterally and straight medially.

**Description.**—♀. *Length.* Body, 8.5 mm. **Head:** Flagellum with 33 flagellomeres. Interantennal space with rounded longitudinal keel, or lacking of longitudinal keel. Antennal sockets deeply excavated, or moderately excavated. Face without me-

dian longitudinal carina. Genae moderately expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum with longitudinal rugosities; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina of propodeum absent. Epicnemial carina sharp, incomplete laterally, straight medially (between forecoxae). Foretibia spines absent. Midtibia with 2–7 (2) spines. Hind tibia with 8–12 (12) spines. Hind femur 3.6 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing present or absent. 2-1A vein of hind wing tubular or not tubular. CUb vein of hind wing not tubular. Hind wing with 4–5 (5) hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.9. Ovipositor 7.2mm. **Color:** Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma with pronotum yellowish orange, sometimes melanic anteriorly; mesoscutum, scutellum and metanotum yellowish orange; propodeum mostly yellowish orange with melanic spots; propleuron yellowish orange or melanic; mesopleuron mostly yellowish orange, melanic basally and metapleuron melanic, or yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange. Hindleg melanic except trochanter and trochantellus yellowish orange. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing banded from base, yellow, infuscate, yellow, infuscate. Metasoma mostly yellow-

ish orange but fourth tergum with median tergum melanic and fifth to eighth terga melanic.

♂.—Essentially as female.

**Material examined.**—*Holotype*. Brasil: ♀, Manaus, Reserva Dulce, 31.viii.1990, Trampa malaise, Vidal col. (INPA). **Paratypes.** Peru: ♂, Puerto Bermúdez, 12–19.vii.1920, Cornell Univ. Expedition (CUIC); ♀, Avispas, 30km nr Marcapata, ix.1992, Luis Peña (AEI).

**Distribution.**—*Sesiocionus galeos* is known only from Brazil and Peru.

**Etymology.**—From Greek *galeos* that means shark in honor of Michael Sharkey, in acknowledgment for his advising in my formation as braconid taxonomist and for his contribution to the knowledge of the Agathidinae of the World.

#### *Sesiocionus garciai* Briceño, sp. n.

**Diagnosis.**—*S. garciai* is known only from one specimen and can be distinguished from all other species by the following combination of characters: occipital tubercles present, occiput excavated, epicnemial carina complete and straight medially, although the presence of spines on the fore tibia.

**Description.**—♀. Length. Body, excluding ovipositor, 6 mm. **Head:** Flagellum with 30 flagellomeres. Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina of propodeum absent. Epicnemial carina sharp, complete, straight

medially (between forecoxae). Foretibia spines present. Midtibia with 9 spines. Hind tibia with 15 spines. Hind femur 3.64 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 4 hamuli. **Metasoma:** Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.9. Ovipositor 5 mm. **Color:** Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange except two basal palpomeres melanic. Mesosoma yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange except tibia and tarsus melanic. Hindleg melanic with coxa yellowish orange femur mostly yellowish orange, but melanic distally. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma tergum yellowish orange except fifth to eighth metasomal terga mostly yellowish orange but median tergites melanic posteriorly. Ovipositor yellowish orange except apical eighth melanic.

♂.—Unknown.

**Material examined.**—*Holotype*. Brasil: ♀, Nova Teutonia, 27°11'N 52°23'L, 2.ii.1939, Fritz Plaumann (CNC).

**Distribution.**—This species is known only from the Nova Teutonia region of Brazil.

**Etymology.**—This species is named in honor of Jose Luis Garcia, Venezuelan entomologist, for his contribution to the knowledge of Venezuela proctotrupoids.

***Sesioctonus grandis* Briceño, sp. n.**

Figs. 19, 29, 36, 37

**Diagnosis.**—*S. grandis* is the larger species of Genus *Sesioctonus* and it has a higher number of flagellomeres (48), maxilla and labium with four palpomeres, and the first metasomal median tergite with depression posterad spiracle. This latter

character is shared with *S. qui* from which it is separated by the presence of an oval-shape subpronope, epicnemial carina absent and the presence of a pair of lateral longitudinal carinae on the first metasomal median tergite.

**Description.**—♀. **Length.** Body, excluding ovipositor, 10–13 mm (10.0). **Head:** Flagellum with 44–48 flagellomeres (46). Inter-antennal space with sharp longitudinal keel. Antennal sockets deeply excavated. Face without median longitudinal carina. Genae strongly expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible flat, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres partly fused. **Metasoma:** Subpronope oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum with longitudinal rugosities; without median longitudinal carina; and lacking lateral carinae. Propodeum convex, median longitudinal carina of propodeum absent. Epicnemial carina completely absent. Foretibia spines absent. Midtibia with 5–8 spines (8). Hind tibia with 14–21 spines (21). Hind femur 4.4 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing absent. 2-1A vein of hind wing not tubular. CUb vein of hind wing not tubular. Hind wing with 8–10 hamuli (9). **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite with depression posterad spiracle. Length width ratio of first metasomal median tergite 0.71. Ovipositor 10 mm. **Color:** Head melanic. Antenna melanic, sometimes yellowish orange. Maxillary and labial palpomeres yellowish orange except two basal palpomeres melanic. Mesosoma melanic. Forelegs yellowish orange except coxa melanic, trochantellus, tibia and tarsus yellowish orange, or melanic. Midlegs yellowish orange except coxae and tarsus melanic. Hindleg melanic. Forewing

banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic, or melanic and yellowish orange. Hind wing yellow basally infuscate apically. Metasoma melanic. Ovipositor yellowish orange.

♂.—Essentially as the female.

*Material examined.*—*Holotype*. Brazil: ♀, Rio Grande do Sul, Staudinger K col. (ZSBS). Paratypes. Brazil: 4♀, 5♂, Rio Grande do Sul, Staudinger K col. (ZSBS) (UCOB).

*Distribution.*—This species is known only from the Rio Grande do Sul region of Brazil.

*Etymology.*—*grandis* refers the big size of these specimens.

***Sesioctonus kompsos* Briceño, sp. n.**

*Diagnosis.*—*S. kompsos* can be distinguished for the following combination of characters: occipital tubercles present, occiput excavated, median areola of metanotum with longitudinal rugosities.

*Description.*—♀. *Length.* Body, excluding ovipositor, 8.0–10.0mm (10). *Head:* Flagellum with 33–34 (34) flagellomeres. Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth of mandible longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. *Mesosoma:* Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum with longitudinal rugosities; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibia spines absent. Midtibia with 9–13 (13) spines. Hind tibia with 21–25 (25) spines. Hind femur 3.2–3.43 (3.2) times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of

forewing absent. 2-1A vein of hind wing tubular. Cub vein of hind wing not tubular. Hind wing with 6 hamuli. *Metasoma:* Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.94–1.20 (0.94). Ovipositor 8 mm. *Color:* Head melanic. Antenna melanic. Maxillary palpomeres yellowish orange except two basal palpomeres melanic. Labial palpomeres melanic. Mesosoma mostly melanic except metanotum, propodeum and metapleuron yellowish orange. Forelegs melanic. Midlegs melanic. Hindleg melanic. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange. Ovipositor yellowish orange except apical eighth melanic.

♂.—Unknown.

*Material examined.*—*Holotype*. Costa Rica: ♀, Rancho Quemado, 2km N. camino Drake, 275m, i.1991, P. Hanson (UCR). *Paratype.* Brasil: ♀, Guanabara, Represa Rio Grande, viii.1966, M. Alvarenga (AEI).

*Distribution.*—This species is known only from Costa Rica and Brazil.

*Etymology.*—From Greek *kompsos* that means elegance in reference to the beauty of this species.

***Sesioctonus miyayensis* Briceño, sp. n.**

*Diagnosis.*—*S. miyayensis* shows the following combination of characters: occipital tubercles absent, subpronope elongate-oval-shaped, median areola of metanotum with lateral carinae meeting posteriorly, epicnemial carinae complete and straight medially, foretibia with spines, first metasomal tergite with pair of lateral longitudinal carinae.

*Description.*—♀. *Length.* Body, excluding ovipositor, 5–7 mm (6.5). *Head:* Flagellum with 32 flagellomeres. Interantennal space with rounded longitudinal keel. Antennal sockets not excavated. Face without median longitudinal carina. Genae moderate-

ly expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible flat, outer tooth of mandible not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:** Subpronope elongate-oval. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina sharp, complete, straight medially (between forecoxae). Foretibia spines present. Midtibia with 5-7 spines (7). Hind tibia with 14 spines. Hind femur 3.42 times as long as wide. (RS+M)a vein of forewing incomplete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 3-4 hamuli (3). **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.1. Ovipositor 5 mm. **Color:** Head yellowish orange. Antenna melanic. Maxillary and labial palpomeres melanic, or yellowish orange except two basal palpomeres melanic. Mesosoma yellowish orange. Forelegs yellowish orange except femur and tibia melanic. Midlegs yellowish orange except tibia yellowish orange basally, otherwise melanic and tarsus melanic with basitarsus yellowish orange in basal half. Hindleg yellowish orange except tibia yellowish orange in basal half, melanic apically and tarsus melanic. Forewing yellow basally and infuscate apically. Stigma melanic, or yellowish orange. Hind wing yellow basally infuscate apically. Metasoma yellowish orange. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—*Holotype*. Costa Rica: ♀, Pto. Viejo, 50m, ii.1980, W. Mason

(AEI). *Paratypes*. Costa Rica: 8♀, Heredia, Est. Biol. La Selva, 10°26'N 84°01'W, 50-150m, xii.1992, P. Hanson (UWY), 1.xi.1993, J. Longino (UK), 01.viii.1995, 15.i.1996, iii.1996, ii.1996, 31.v.1996, 19.ii.1998 (UK); ♀, Prov. Guanacaste, Est. Pitilla 9km S. Sta. Cecilia, 700m, 4-14.xi.1991, D. García (INBio); ♀, Prov. Puntarenas, Rancho Quemado, Península de Osa, 200m, vi.1992. F. Quesada y M. Segura (INBio).

**Distribution.**—This species is known only from Costa Rica.

**Etymology.**—This species is named in honor of my father's birthplace, Miyayi.

### *Sesioctonus parathyridis* Viereck

*Sesioctonus parathyridis* Viereck 1912: 1, ♀, "Paraiso, Canal de Panamá" (Washington, ♀, 14552).—Busk 1912: 10, fig. (host a). Host a: *Parathyridis perspicilla* Stoll.

**Diagnosis.**—*S. parathyridis* shares characters with *S. grandis* and *S. qui*. They conform the group of species with the larger size and the number of flagellomeres more than 40. Also, they have the interantennal space with a longitudinal sharp keel, which is present in *S. acrolophus*. However, *S. parathyridis* can be separated from these species by the presence of a pair of lateral longitudinal carinae on the median tergite of first metasomal segment. This character is shared with *S. grandis*. However, this latter species has the first metasomal segment with a depression posterad spiracle, which are absent in *parathyridis*.

**Description.**—♀. **Length.** Body, excluding ovipositor, 9-12 mm (12.0). **Head:** Flagellum with 44-45 flagellomeres (42). Interantennal space with sharp longitudinal keel. Antennal sockets deeply excavated. Face without median longitudinal carina. Genae strongly expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible flat, outer tooth not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. **Mesosoma:**

Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum with longitudinal rugosities; without median longitudinal carina; and lacking lateral carinae. Propodeum flat, median longitudinal carina absent. Epicnemial carina blunt, incomplete laterally, bilobed medially (between forecoxae). Foretibia spines absent. Midtibia with 5–8 spines (6). Hind tibia with 14–16 spines (14). Hind femur 4.88 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing present. 2-1A vein of hind wing not tubular. CUb vein of hind wing not tubular. Hind wing with 7–8 hamuli (7). *Metasoma*: Median tergite of first metasomal segment with pair of lateral longitudinal carinae, or without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.8. Ovipositor 10–12 mm (12.0). *Color*: Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange except two basal palpomeres melanic. Pronotum mostly melanic with yellowish orange areas. Mesoscutum yellowish orange, or mostly melanic, yellowish orange dorsally. Scutellum yellowish orange. Metanotum yellowish orange. Propodeum yellowish orange, or mostly yellowish orange with melanic spots. Propleuron mostly melanic with yellowish orange areas, or yellowish orange. Mesopleuron yellowish orange. Metapleuron yellowish orange. Forelegs mostly yellowish orange except femur melanic; tibia yellowish orange, or melanic but yellowish orange distally and tarsus mostly yellowish orange, but apical tarsomere melanic. Midlegs mostly yellowish orange with variations on coxa sometimes melanic apically; femur yellowish orange in basal half, melanic apically; tibia yellowish orange in basal half, melanic apically, or yellowish orange and tarsus melanic. Hindleg melanic except coxa yellowish orange in basal half, me-

lanic apically. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing yellow basally infuscate apically. Metasoma yellowish orange except the last four segments yellowish orange or melanic. Ovipositor yellowish orange except apical eighth melanic.

♂.—Essentially as the female.

*Material examined*.—*Holotype*. Panama: ♀, Paraíso, Canal de Panama, host: *Parathyris perspicilla* Stoll (USNM). *Another specimen reviewed*. Panama: ♀, Barro Colorado Is., 9°9'N 79°51'W, 2–9.x.1996, J. Pickering (UK); Costa Rica: 2♀, ♂, Prov. Limón, Sector Cerro Cocorí, Finca de E. Rojas, 150m, 26.vi–16.vii.1992, 12–31.viii.1992, ii.1993, E. Rojas (INBio); ♀, Prov. Puntarenas, Est. Sirena, P.N. Corcovado, 0–100m, ii.1992, G. Rodríguez (INBio); ♀, Prov. Puntarenas, Vuelta Campana, R. Terraba, 100–150m, 10–31.viii.1992, S. Rojas (INBio); Peru: Loreto, Pucallpa, 24.vi.1963, J. M. Schunke (BMHN).

*Distribution*.—This species is distributed from Costa Rica and Panamá in Central America to Peru in South America.

*Biology*.—Larvae of *Sesioctonus parathyridis* were reported as parasitoids in larvae of the arctiid *Parathyris perspicilla* (Viereck 1914).

#### *Sesioctonus peruviensis* Briceño, sp. n.

*Diagnosis*.—*S. peruviensis* is known only from one specimen, however, can be distinguished from all other species by the following combination of characters: maxilla with four palpomeres and labium with three, occipital tubercles present, occiput excavated, foretibia with spines. Specimens of *peruviensis* could be confused with *S. garciai* specimens, however they are separated for the presence of epicnemial carinae bilobed in *S. peruviensis*, which is straight in *S. garciai*.

*Description*.—♀. Length. Body, excluding ovipositor, 5.5 mm. *Head*: Flagellum with 31 flagellomeres. Interantennal space with rounded longitudinal keel. Antennal sock-

ets moderately excavated. Face without median longitudinal carina. Genae moderately expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave, outer tooth longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. *Mesosoma*: Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum convex, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibia spines present. Midtibia with 10 spines. Hind tibia with 18 spines. Hind femur 3.27 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing present. 2-1A vein of hind wing not tubular. CUb vein of hind wing not tubular. Hind wing with 4 hamuli. *Metasoma*: Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Ovipositor 5 mm. *Color*: Head melanic. Antenna melanic. Maxillary palpomeres yellowish orange except basal two palpomeres melanic. Labial palpomeres melanic. Mesosoma yellowish orange. Forelegs yellowish orange except trochantellus melanic, femur yellowish orange, melanic basally and tarsus mostly yellowish orange, but apical tarsomere melanic. Midlegs yellowish orange except trochanter, tibia and tarsus melanic. Hindleg mostly melanic except coxa yellowish orange and femur yellowish orange, melanic basally. Forewing infuscate with hyaline spots. Stigma melanic. Hind wing entirely infuscate. Metasoma yellowish orange. Ovipositor yellowish orange except apical eighth melanic.

♂.—Unknown.

*Material examined*.—*Holotype*. Peru: ♀, Quincemil, 750m near Marcapata, 20-30.x.1962, Luis Peña (AEI).

*Distribution*.—Known only from Marcapata, region of Peru.

*Etymology*.—This species is named after the country of the holotype specimen.

*Sesiocotinus qui* Briceño, sp. n.

*Diagnosis*.—*S. qui* is distinguished from all other species for the following combination of characters: occipital tubercles absent, interantennal space with a sharp longitudinal keel, gena strongly expanded posteroventrally, median areola of metanotum with longitudinal rugosities and first metasomal median tergite with depression posterad spiracle.

*Description*.—♀. *Length*. Body, excluding ovipositor, 10-15 mm (10.0). *Head*: Flagellum with 45 flagellomeres. Interantennal space with sharp longitudinal keel. Antennal sockets deeply excavated. Face without median longitudinal carina. Genae strongly expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible flat, outer tooth not longer than inner tooth. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. *Mesosoma*: Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum with longitudinal rugosities; without median longitudinal carina; and lacking lateral carinae. Propodeum convex, median longitudinal carina absent. Epicnemial carina, blunt, incomplete laterally, or completely absent, bilobed medially (between forecoxae). Foretibial spines absent. Midtibia with 5-8 spines (5). Hind tibia with 14-16 spines (14). Hind femur 4.27 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing absent. 2-1A vein of hind wing tubular. CUb vein of hind wing not tubular. Hind wing with 8 hamuli. *Metasoma*: Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite with depression posterad spiracle. Length width ratio of first metasomal median tergite 0.84. Ovipositor

10–12 mm (10.0). **Color:** Head melanic. Antenna melanic. Maxillary and labial palpomeres yellowish orange except basal two palpomeres melanic. Mesosoma yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange. Hindleg melanic except coxa yellowish orange but melanic laterally, hind femur yellowish orange, hind tibia yellowish orange in basal half, melanic apically. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma yellowish orange. Hind wing yellow basally infuscate apically. Metasoma yellowish orange with the last four tergites melanic. Ovipositor yellowish orange.

♂.—Male exhibits a color darker than females, showing the body brownish. However, only one male of this species was examined for this revision and another future observations are necessary.

**Material examined.**—*Holotype*: Venezuela: ♀, Aragua, El Limón, 450m, 25.vi.1978, luz de mercurio, Francisco Fernández Yépez col (MIZA). *Paratypes*: Brasil: 2♀, São Paulo, Teodoro Sampaio, xii.1977, F. M. Oliveira (CNC) (BMNH); Peru: ♀, ♂, Loreto, Pucallpa, 19.iv.1962, vi.1965, J. M. Schunke (BMNH).

**Distribution.**—This species is distributed from Venezuela until Brazil and Peru in South America. Its presence in Colombia, Ecuador and Bolivia is probable.

**Etymology.**—The species name *qui* is an arbitrary combination of letters.

### *Sesiocrotus theskelos* Briceño, sp. n.

**Diagnosis.**—*S. theskelos* can be distinguished for the following characters combination: lacking of occipital tubercles, maxilla with 5 palpomeres and labial with 4, median longitudinal carina of propodeum present, and median tergite of first metasomal segment with pair of lateral longitudinal carinae.

**Description.**—♀. **Length.** Body, excluding ovipositor, 7 mm. **Head:** Flagellum with 35 flagellomeres. Interantennal space with rounded longitudinal keel. Antennal sock-

ets moderately excavated. Face without median longitudinal carina. Genae moderately expanded posteroventrally. Occipital tubercles absent. Occiput not excavated. Mandible concave, outer tooth of mandible not longer than inner tooth. Maxilla with 5 palpomeres. Third and fourth labial palpomeres not fused. **Mesosoma:** Subpronope triangular. Longitudinal carinae of scutellar depression absent. Scutellum convex. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum convex, median longitudinal carina present. Epicnemial carina sharp, complete laterally, bilobed medially (between forecoxae). Foretibia spines absent. Midtibia with 6–9 spines (9). Hind tibia with 12–15 spines (12). Hind femur 3.5 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing present or absent. 2-1A vein of hind wing tubular or not tubular. CUB vein of hind wing not tubular. Hind wing with 3–4 (4) hamuli. **Metasoma:** Median tergite of first metasomal segment with pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 0.94–1.12 (0.94). Ovipositor 5–6 mm (5.5). **Color:** Head melanic sometimes with a spot yellowish orange on the front. Antenna melanic. Maxillary and labial palpomeres yellowish orange. Mesosoma yellowish orange. Forelegs yellowish orange. Midlegs yellowish orange except tarsus melanic. Hindleg melanic except coxa yellowish orange, or yellowish orange but melanic laterally; and femur yellowish orange, sometimes melanic distally. Forewing entirely infuscate. Stigma melanic. Hind wing entirely infuscate. Metasoma entirely yellowish orange or yellowish orange with the last four tergites melanic posteriorly. Ovipositor yellowish orange.

♂.—Unknown.

**Material examined.**—*Holotype*: Brasil: ♀,

Matogrosso, Sinop, x.1975, Trampa malaise, M. Alvarenga (CNC). Paratypes. Brasil: ♀, Matogrosso, Sinop, x.1975, Trampa malaise, M. Alvarenga (CNC); Ecuador: ♀, Coca, v.1992, Luis Peña (AEI).

*Distribution.*—This species is known only from Brazil and Ecuador.

*Etymology.*—The species name *theskelos* means wonderful.

### *Sesiocromus venezuelensis* Briceño, sp. n.

*Diagnosis.*—*S. venezuelensis* is the only one species that shows five longitudinal carinae on the scutellar depression, in combination with the presence of occipital tubercles and occiput excavate.

*Description.*—♂. *Length.* Body, excluding ovipositor, 8 mm. *Head:* Flagellum with broken after flagellomere 28. Interantennal space with rounded longitudinal keel. Antennal sockets moderately excavated. Face without median longitudinal carina. Genae not expanded posteroventrally. Occipital tubercles present. Occiput excavated. Mandible concave. Maxilla with 4 palpomeres. Third and fourth labial palpomeres completely fused. *Mesosoma:* Subpronope oval. Longitudinal carinae of scutellar depression present. Scutellum flat. Median areola of metanotum smooth; without median longitudinal carina; and with lateral carinae present and not meeting posteriorly. Propodeum flat, median longitudinal carina absent. Epicnemial carina sharp, complete, bilobed medially (between forecoxae). Foretibia spines absent. Midtibia with 7 spines. Hind tibia with 16 spines. Hind femur 3.5 times as long as wide. (RS+M)a vein of forewing complete. 3RSa vein of forewing present. 2-1A vein of hind wing not tubular. CUB vein of hind wing not tubular. Hind wing with 5 hamuli. *Metasoma:* Median tergite of first metasomal segment without pair of lateral longitudinal carinae. First metasomal median tergite without depression posterad spiracle. Length width ratio of first metasomal median tergite 1.28. *Color:* Head melanic. Antenna melanic. Maxil-

lary and labial palpomeres yellowish orange. Mesosoma melanic. Forelegs yellowish orange except coxa melanic. Midlegs yellowish orange except coxa, trochanter and trocantellus melanic. Hindleg melanic except femur melanic but yellowish orange apically. Forewing banded from base, yellow, infuscate, yellow, infuscate. Stigma melanic. Hind wing banded from base, yellow, infuscate, yellow, infuscate. Metasoma yellowish orange with third tergum yellowish orange but median tergite melanic in posterior quarter and fourth and fifth tergum melanic.

♀.—Unknown.

*Material examined.*—*Holotype.* Venezuela: ♂, Aragua Est. Exp. Cataurito, 32km E Villa de Cura, 1100m, 28.vi.1983, O. S. Flint, Jr. (CNC).

*Distribution.*—This species is known only from the Aragua region of Venezuela.

*Etymology.*—This species is named after the country of the holotype specimen.

### ACKNOWLEDGMENTS

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## The Effect of Body Size on Male-Male Combat in the Parasitoid Wasp *Melittobia digitata* Dahms (Hymenoptera: Eulophidae)

CHRISTOPHER S. HARTLEY AND ROBERT W. MATTHEWS

University of Georgia, Department of Entomology, Athens, GA 30602-2603, USA,  
CSH email: chartley@uga.edu; RWM email: rmatthew@uga.edu

**Abstract.**—The parasitic wasp *Melittobia digitata* Dahms (Hymenoptera: Eulophidae) is a gregarious external parasitoid of various insects, primarily solitary wasps and bees. Males of *M. digitata* commonly engage in fierce, often fatal, fights with other males. The mandibles are the main weapons used, and injuries inflicted vary greatly in severity from loss of appendages to death. We investigated the effect of size differences between winning, losing, and non-fighting males and whether body size was related to being a fighter or non-fighter. The head width and tibia length of fighting and non-fighting males were measured. Winning males (21 of 29 pairs) were found to be larger than losing males, and fighting males (winners and losers combined) were found to be larger than non-fighting males (8 pairs). Mandible lengths of a subset of all males (15 fighters, 12 non-fighters) were subsequently measured; only fighter's left mandible length was significantly correlated with head width. The possibility that two behavioral forms (fighters and non-fighters) exist is considered but will require further experiments to resolve.

Ritualized fighting over food, territory, mates and other resources occurs between males in the majority of animal species. Many studies have emphasized the restrained nature of male fights by showing that the majority of fights end peacefully with neither combatant being injured, even in species where the males possess large and dangerous weapons (Maynard Smith and Price 1973; Maynard Smith 1982). In addition, fighting males often display striking dimorphisms such as those found in certain beetles (Forsyth and Alcock 1990; Zeh et al. 1992; Goldsmith and Alcock 1993) and mites (Saito 1990, 1995). Instances of fatal fighting have been observed in some animal species. Where they do occur, fatal fights usually involve opportunities to mate, and they are limited to species where males have limited opportunities to mate (Enquist and Leimar 1990). Fatal fighting has been well documented in many fig wasps (Hamilton 1979; Murray 1987; Bean and Cook 2001). These wasps spend their entire life within

the swollen inflorescences of various fig species, and fights occur between well-armored flightless males that pursue newly emerged females. The majority of males do not emerge from the fig in which they are born though emergence is more common in some species (Bean and Cook 2001). Males have also been shown to have a strong attraction to the fig in which they were reared (Frank 1985), which makes dispersal unlikely. Since potential mating opportunities are limited, fights between males are fierce and result in many fatalities.

*Melittobia digitata* Dahms (Hymenoptera: Eulophidae) is a gregarious external parasitoid of many different insects, but its principal hosts are solitary wasps and bees. In the southeastern United States, *M. digitata* is most commonly found attacking the mud dauber wasp, *Trypoxyylon politum* Say (Hymenoptera: Sphecidae). A female *Melittobia* enters a *Trypoxyylon* cocoon before it is sealed and waits until the host transforms into a prepupa before ovipos-

iting hundreds of eggs directly onto the prepupa's cuticle (Dahms 1984; González and Terán 2001). Upon hatching, the gregariously developing *Melittobia* larvae consume the host, complete their development and begin to emerge in approximately 20 days, depending on temperature. The average brood size for *M. digitata* resulting from one female foundress is 522 young. Males and females emerge together, but the sex ratio is extremely female biased—about 98% female (J.M. González, personal communication). Females characteristically mate once, usually soon after emergence, and one male may mate with numerous females in his lifetime. Mated females then chew their way out of the host's cell and disperse to search for new hosts (Dahms 1984).

Sexual dimorphism is extreme in *Melittobia*. Adult males possess vestigial eyes, short non-functional wings, enlarged antennal scapes, and mandibles with well-developed teeth. The blind males wander freely inside the host's cocoon until they encounter a female or another male. Encounters with females instigate courting and mating behaviors, and virgin females often gather in groups around males to await mating (González et al. 1985; Consóli et al. 2002). Encounters with other males quickly escalate into a grappling contest where the males interlock their legs and struggle briefly with each other. Following these bouts, the males will either separate or attempt to use their mandibles to tear at the body of the opponent. These fights often lead to loss of appendages and death in one or both fighters (Dahms 1984). Inside naturally parasitized mud dauber cocoons, one routinely finds the remains of several males, many dismembered. In most laboratory cultures of *M. digitata*, males grapple and fight with little provocation, and these contests frequently end with the death of one or both combatants. In other cultures, we have found many males alive with no injuries and no evidence of fighting. Long term

culturing in the laboratory does not alter *Melittobia* behavior (Assem and Jachmann 1999), so intense fighting is not likely to be an artifact of mass rearing.

The occurrence of fatal fighting in both fig wasps and *Melittobia* is unexpected because males are normally fighting their brothers. Hamilton (1979) suggested that fighting behavior would not exist where a male's rival has a high chance of being a brother. Recent work with fig wasps, however, found no relationship between relatedness of males and fighting behavior. It was found instead that the level of fatal fighting was negatively correlated with future mating opportunities (West et al. 2001). A similar situation exists in *Melittobia* where males have little chance of future mating opportunities since they are not likely to disperse.

The objective of this study was to determine if size differences exist in *M. digitata* between winners and losers of fights and between fighting and non-fighting males. We hypothesized that winners would be larger than losers and that fighters would be larger than non-fighters.

## MATERIALS AND METHODS

*Melittobia digitata* cultures were reared in an incubator at 25°C on *T. politum* prepupae in small plastic boxes (5cm × 2.5cm × 1.8cm) with tightly fitting lids. Males were removed from cultures as pupae and isolated in Carolina™ clear Deep Well Projection Slides (25 mm diameter, 2 mm deep). This isolation ensured that a male's age and prior mating and fighting experience could be controlled. No data were recorded on male emergence time relative to other males from a particular culture nor from which culture a given male emerged. Thus, males used in the experiments can be regarded as arbitrarily selected from among a range of males available.

When the males isolated in the depression slides emerged, the date of their emergence was recorded. Eighty-seven

Table 1. Morphometric measurements of *M. digitata* males.

	Total number	Mean tibia length*	Mean head width*
Winners	21	0.25 ± 0.03	0.35 ± 0.04
Losers	21	0.23 ± 0.03	0.34 ± 0.04
Fighters	42	0.24 ± 0.03	0.35 ± 0.04
Non-Fighters	16	0.20 ± 0.03	0.29 ± 0.03

\* Values in mm ± Standard Deviation.

males were kept isolated and observed daily, and their date of death was recorded. These males served as controls for the following experiment.

Twenty-nine newly emerged male pairs were formed in the depression slides by opening the two individual slides and using a paintbrush to move one of the males into the other male's slide. Because of the difficulty of marking individuals, it was not possible to track which male was resident versus intruder in the pairings. Once each pair had been formed, the slides were not opened again until after both males had died. Each pair was observed daily, and the date of each male's death was recorded.

After death, each male was examined, and any obvious injury (e.g., loss of appendages, body wounds) was recorded. The head and right front tibia of each male were then mounted temporarily in glycerol on standard glass microscope slides and measured under 50 $\times$  magnification using an ocular micrometer. Both males of one pair were mounted on the same slide so that winners and losers could be associated. To avoid crushing the specimens, pieces of 6lb. test nylon fishing line were placed around them to elevate the cover slip.

To test whether head width is correlated with mandible length, 15 fighter heads and 12 non-fighter heads were arbitrarily selected, and their mandibles were dissected. Both left and right mandibles were mounted on microscope slides and their maximum length was measured.

Sign tests were used to analyze winner

versus loser data so that both males of one fighting pair could be compared against each other. Mann-Whitney U tests were used to analyze fighter versus non-fighter data. Spearman R Correlations were used for all correlations. A *P* value of 0.05 was taken as the critical value for establishing significance. Analyses were done using STATISTICA 6 © StatSoft, Inc.

## RESULTS

In 21 of the pairs, one male killed the other in a fight. These males were termed fighters. In eight of the pairs, the males were never observed to come into contact with each other, and after death neither male was found to have lost appendages or incurred wounds to the body. We concluded in these cases that no fighting had occurred, and these males were recorded as non-fighters.

Table 1 shows the measurement data for all males.

Winners had significantly longer tibia ( $Z = 2.29$ ;  $P = 0.022$ ), but head widths of winners and losers did not differ significantly ( $Z = 1.21$ ;  $P = 0.228$ ). The tibia length of all fighters (winners and losers combined) was significantly longer than the non-fighters' tibia length ( $U = 134.0$ ;  $Z = 3.58$ ;  $P < 0.001$ ), and fighters' heads were significantly wider than non-fighters' ( $U = 88.5$ ;  $Z = 4.34$ ;  $P < 0.001$ ). Head width and tibia length for all males (fighter and non-fighter) were significantly correlated ( $\rho = 0.665$ ;  $P < 0.001$ ).

The only significant correlation between head width and mandible length was found for fighters' left mandibles ( $\rho =$

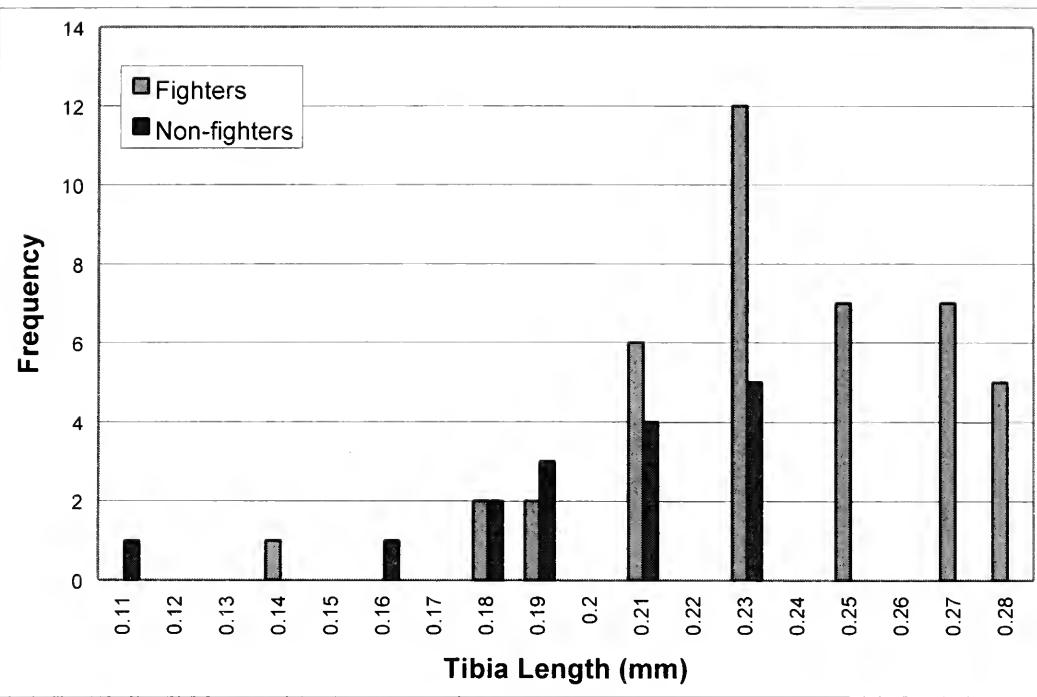


Fig. 1. Frequency distribution for tibia length comparing all fighters and non-fighters ( $n = 58$ ).

0.692;  $P = 0.004$ ). Fighters' right mandibles were not significantly correlated with head width ( $\rho = 0.351$ ;  $P = 0.200$ ). Non-fighters' left mandibles were not significantly correlated with head width ( $\rho = 0.507$ ;  $P = 0.092$ ), and non-fighters' right mandibles were not significantly correlated with head width ( $\rho = 0.452$ ;  $P = 0.140$ ).

Differences in size between fighters and non-fighters and the obvious behavioral differences suggested the possibility that the *Melittobia* male population could be dimorphic. To explore this possibility, frequency distributions of the measurements of tibia length and head width were prepared (Figs. 1 and 2). If a dimorphism exists, a bimodal curve is expected. The graph of tibia length frequency reveals only one peak for both fighters and non-fighters, and this peak occurs at 0.23 mm. The graph of head width frequencies suggests the presence of two peaks—one for non-fighters at 0.28 mm and one for fighters at 0.37 mm. There is, however, consider-

erable overlap, and values for fighters and non-fighters occur at both ends of the scale.

## DISCUSSION

We predicted that winners would be the larger males. The results revealed that winners were larger than losers based on their tibia length measurements, although their head widths did not differ. The correlation between head width and tibia length suggests that relative size of either is likely to be a good predictor of overall body size, which in turn is related to fighting success. Mandible size has been often discussed in relation to fighting fig wasps (Bean and Cook 2001). The frequent asymmetry between right and left mandible lengths in our study was unexpected, and may be interesting to pursue.

The existence of non-fighter males, in which paired males never engaged in a fight even though they were isolated together for their whole life, raises the pos-

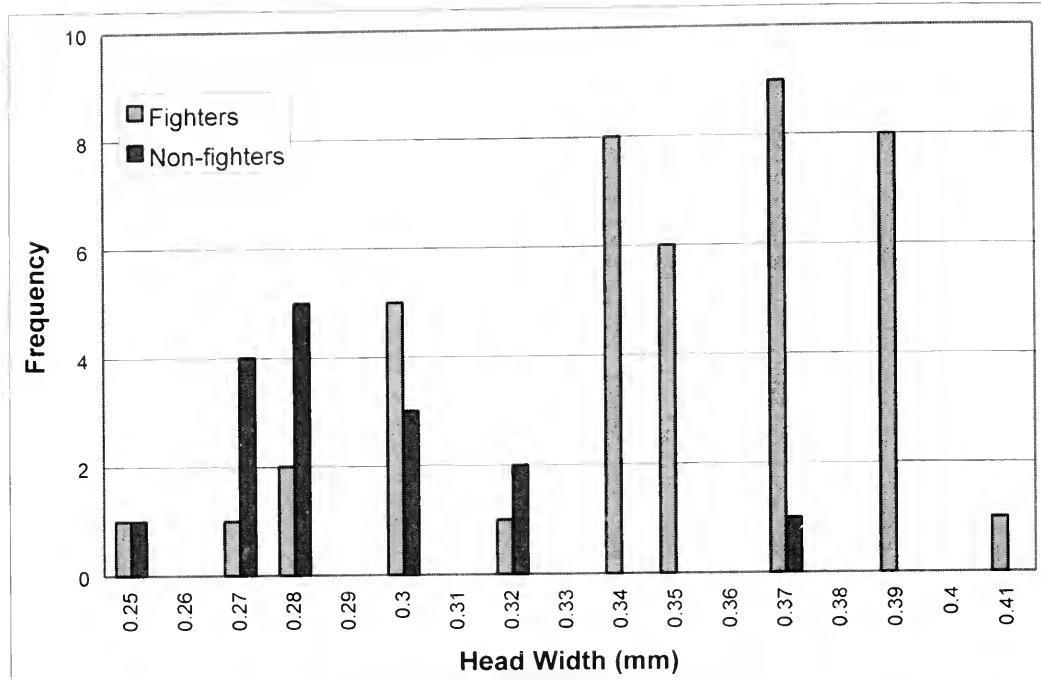


Fig. 2. Frequency distribution for head width comparing all fighters and non-fighters ( $n = 58$ ).

sibility that males exist in two behavioral morphs. Freeman and Ittyeipe (1982) described two morphologically distinct male morphs in *Melittobia hawaiiensis* Perkins (= *M. australica* Girault): a larger morph with ocelli and a smaller morph without ocelli. However, we found that all of our *M. digittata* males, large and small, had fully pigmented ocelli. The frequency graphs of head width and tibia length (Figs. 1 and 2), while showing a trend towards a bimodal distribution for each trait, also reveal that a wide range of sizes exists in both fighting and non-fighting males. Overall, most of the larger males became fighters while most of the smaller males never engaged in fights, but there were obvious exceptions. Perhaps fighting and non-fighting are conditional rather than fixed traits. Alternatively, there could be culture or lineage specific effects on the likelihood of a male becoming a fighter or non-fighter. These questions will require further investigation.

Abe et al. (2003) found that when an emerged male and a pupal male were placed together, the already emerged male usually killed the pupal male at or immediately after eclosion, but they did not record sizes of any of the males in their experiment. We have noted that the first males to emerge are generally larger most likely due to better food quality and quantity, and small males emerge later in the culture's life, when the host is covered with developing pupae (unpublished data). Males of different fig wasp species are known to exist in a wide variety of body shapes, each with a different fighting propensity, and each is adapted to courting females in a different way (Murray 1990). If fighting behavior in *Melittobia* is linked to size, then perhaps a similar situation occurs with small, non-fighting males being better adapted to maneuvering amongst the developing pupae in the tightly packed confines of a *Trypoxylon* cocoon. They could avoid the stress of fight-

ing by staying hidden, but they could still court females. Repeating these experiments using males from one culture and tracking relative emergence times could help to determine if males that emerge early tend to be larger and become fighters and males that emerge late tend to be smaller and become non-fighters.

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## Morphological Variation in *Opius* Wesmael (Hymenoptera: Braconidae) with an Emphasis on Nearctic Species in the Subgenus *Gastrosema* Fischer

ROBERT R. KULA

Department of Entomology, Texas A&M University, College Station, TX, USA 77843,  
email: rkula@oznet.ksu.edu

**Abstract.**—The variability of morphological characters and their potential phylogenetic utility in Opiinae are evaluated using Nearctic species in the subgenus *Gastrosema* Fischer. Diagnoses for three species groups within Nearctic *Gastrosema* are provided, and 43 Nearctic species in *Opius* Wesmael are placed in the species groups. Two new Nearctic species in *Gastrosema* are described: *Opius abbyae* Kula and *O. lacopitaensis* Kula. Five previously described Nearctic species in *Gastrosema* are redescribed: *O. castaneigaster* Fischer, *O. intermissus* Fischer, *O. oscinidus* (Ashmead), *O. saluonensis* Fischer, and *O. striativentris* Gahan. *Opius gracillariae* Gahan is designated a junior synonym of *O. striativentris*.

Opiinae is a very large subfamily in Braconidae with approximately 1,500 described species worldwide (Wharton 1997b). All valid rearing data suggest that species in Opiinae are strict koinobiont endoparasitoids of cyclorrhaphous Diptera (Wharton 1999). *Opius* Wesmael is the largest genus in Opiinae, and over 1,000 species are currently placed in *Opius* sensu Fischer (1972). In a series of regional revisions, Fischer (1972, 1977, 1987) segregated species in *Opius* into 27, 30, and 34 subgenera, respectively. Most of the subgenera are broadly defined and lack features that clearly characterize them as monophyletic. Further, the defining feature of several subgenera, including *Gastrosema* Fischer, *Merotrachys* Fischer, *Phaeodrotoma* Förster sensu Fischer (1972), and *Tolbia* Cameron sensu Fischer (1972), is the presence or absence of sculpture associated with specific anatomical features. Intraspecific variation of sculpture has never been assessed for species in these subgenera, and preliminary sorting indicates that certain species fit the concept of more than one subgenus. Therefore, the morpholog-

ical limits of these subgenera need to be evaluated. This research begins to address these problems by performing a detailed assessment of intraspecific morphological variation for Nearctic species in *Gastrosema*.

Other than Fischer's (1977) revision of New World Opiinae, there has been little work on Nearctic species in *Gastrosema*. Gahan (1915) described two Nearctic species currently included in *Gastrosema* and provided a key to the North American species in *Opius*. Fischer (1964, 1970) described several Nearctic species in *Opius* that were subsequently placed in *Gastrosema* by Fischer (1977). Marsh (1974) synonymized two Nearctic species in *Gastrosema*, but insufficient material was examined to assess intraspecific morphological variation. Additional specimens must be acquired and compared with the holotypes to confirm Marsh's synonymies. Van Achterberg (1997) transferred *O. pumilio* Wesmael (the type species for *Gastrosema*) to *Phaeodrotoma* sensu van Achterberg and Salvo (1997). This action suggests that van Achterberg (1997) treated *Gastrosema* Fi-

scher 1972 as a junior synonym of *Phaedrotoma* Förster 1862, although this was not explicitly stated. Since only some species currently classified as *Gastrosema* possess the characters used to define *Phaedrotoma* *sensu* van Achterberg and Salvo (1997), synonymy seems inappropriate. Additionally, *Phaedrotoma* *sensu* van Achterberg and Salvo (1997) is partially defined by the absence of a basal mandibular tooth which the authors regarded as plesiomorphic. It appears that *Phaedrotoma* *sensu* van Achterberg and Salvo (1997) has not been defined as a monophyletic group, and I see no advantage in accepting the changes proposed by van Achterberg (1997) over Fischer's (1972) concept of *Gastrosema*.

#### MATERIALS AND METHODS

Specimens used in this study were borrowed from several North American museums and collections. The American Entomological Institute (AEI), the California Academy of Sciences (CAS), the Canadian National Collection of Insects (CNCI), the Insect Research Collection at the University of Wisconsin-Madison (IRCW), the Museum of Comparative Zoology at Harvard University (MCZ), the insect collection at Texas A&M University (TAMU), and the United States National Museum of Natural History (USNM) provided determined and undetermined opiines. In addition to the borrowed material, two opiine species treated in this study were reared from isolated puparia. Dr. Sonja J. Scheffer provided several hundred specimens of *O. striativentris* Gahan reared from five species of *Phytomyza* Fallén mining the leaves of seven species of *Ilex* L. (holly). Eighteen specimens of an undescribed opiine were reared by the author from a species of *Calycomyza* Hendel mining the leaves of *Helianthus annuus* L. (sunflower).

Species treated in this study can be identified to Opiinae using Sharkey (1997) and to *Opius* using Wharton (1997a). Sev-

eral hundred Nearctic species in at least 11 subgenera have not yet been examined but potentially fall into the species groups treated in this paper. As a result a comprehensive key to the Nearctic species in each species group cannot be provided at this time. Therefore, a detailed diagnosis is provided for each species group and species to facilitate their identification.

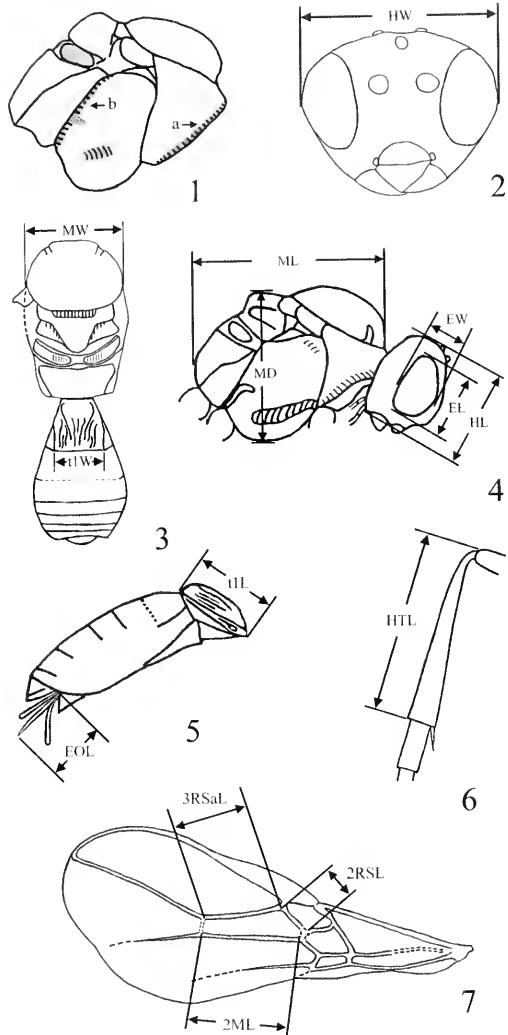
Descriptive terminology for anatomical features, including wing cells and veins, is based on Sharkey and Wharton (1997). Terminology used to describe surface sculpture follows Harris (1979) and Sharkey and Wharton (1997). Two anatomical terms used throughout this work are not found in Harris (1979) or Sharkey and Wharton (1997). Both terms must be defined and illustrated to provide maximum clarification. The anterior pronotal furrow is a groove located at the antero-lateral edge of the pronotum just posterior to the propleural flange, and the posterior mesopleural furrow is a groove located at the posterior edge of the mesopleuron just anterior to the metapleuron (Fig. 1).

Several measurements were taken to quantitatively characterize each species described or redescribed in this study (Figs. 2-7). Two criteria were used to select measurements: 1) measurements historically used in opiine species descriptions and 2) measurements that describe the general size and shape of each species.

#### MORPHOLOGICAL VARIATION

Results from the analysis of intraspecific morphological variation provide a basis for discussing character variability and their potential phylogenetic utility in Opiinae. The following section is an assessment of characters potentially useful for supporting monophyletic groups, as well as characters useful for defining the limits of species.

*Size and shape of clypeus.*—Fischer (1972) used the exposure of the labrum in frontal view (a result of clypeus length) to partially define certain subgenera. For exam-



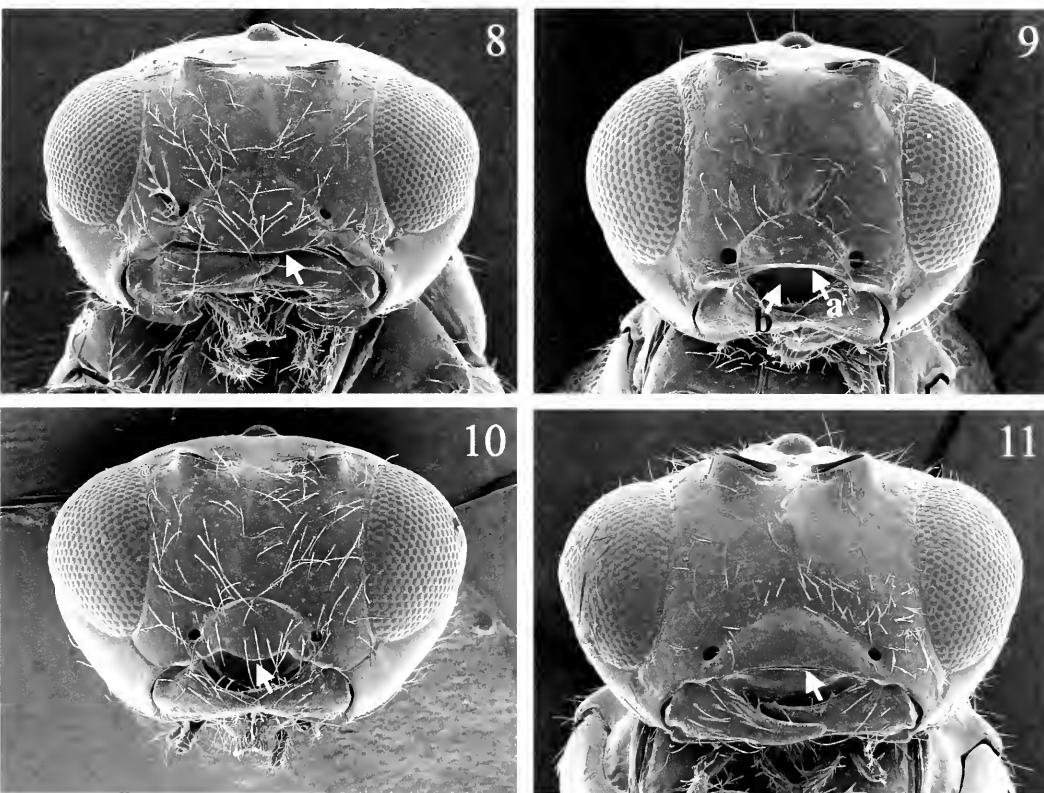
Figs. 1–7. 1, Anterior pronotal furrow (arrow a) and posterior mesopleural furrow (arrow b). 2, Head width (HW). 3, Mesosoma width (MW) and tergite 1 width (t1W). 4, Head length (HL), eye length (EL), eye width (EW), mesosoma length (ML), and mesosoma depth (MD). 5, Tergite 1 length (t1L) and exposed ovipositor length (EOL). 6, Hind tibia length (HTL). 7, 2RS length (2RSL), 3RSa length (3RSaL), and 2M length (2ML). Figs. 1 and 3–5 modified from Fischer (1972).

ple, species that Fischer included in *Stomosema* Fischer possess a broad clypeus completely concealing the labrum (Fig. 8). Alternatively, species that Fischer included in *Gastrosema* have a reduced clypeus

exposing the labrum in frontal view (Fig. 9).

Three basic clypeal morphologies are observed among Nearctic species in *Gastrosema*. Both *O. oscinidis* (Ashmead) and *O. walleyi* Fischer possess a flattened or convex clypeus with the ventral margin lobed mesally (Fig. 10). This condition is also commonly observed for Nearctic species in *Rhogadopsis* Brèthes *sensu* Wharton (1987) and *Thoracosema* Fischer. *Opius striativentris* possesses a convex, hemispherical to narrowly hemielliptical shaped clypeus with a straight to slightly arched ventral margin (Fig. 9). This is the most commonly observed clypeal shape for Nearctic species in *Gastrosema* and is also commonly observed for Nearctic species in *Phaedrotoma* *sensu* Fischer (1972) and *Tolbia* *sensu* Fischer (1972). Both *O. flavigeps* Gahan and *O. salmonensis* Fischer possess a flattened, broadly hemielliptical shaped clypeus with a straight to slightly arched ventral margin (Fig. 11). This clypeal shape is also commonly observed for Nearctic species in *Pleurosema* Fischer. The consistency of clypeus size and shape within a species, coupled with the variability of clypeus size and shape among groups of species, suggests that this character is potentially phylogenetically informative and merits consideration in future phylogenetic analyses.

*Shape of mandibles.*—Mandible shape is another feature Fischer (1972) used to partially define certain subgenera. For example, *Opiognathus* Fischer and *Opiostomus* Fischer contain species with mandibles that are abruptly widened distally to proximally (basal tooth present) (Fig. 12). In more recent revisionary work, van Achterberg and Salvo (1997) used mandible shape to split *Opius* *sensu lato* into two genera: *Opius* and *Phaedrotoma*. *Opius* *sensu* van Achterberg and Salvo (1997) includes species that possess a distinct basal tooth, while *Phaedrotoma* *sensu* van Achterberg and Salvo (1997) includes species that lack a distinct basal tooth (Fig. 13).

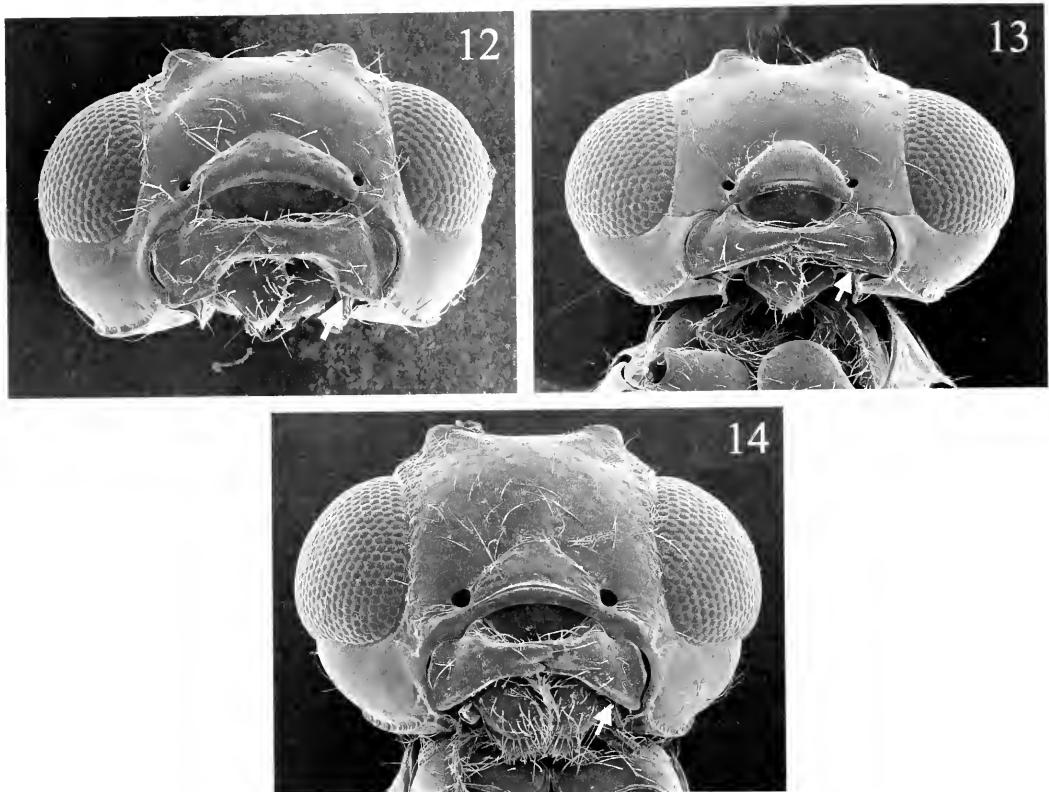


Figs. 8–11. Size and shape of clypeus. 8, Broad and completely concealing labrum. 9, Reduced (arrow a) and exposing labrum (arrow b). 10, Ventral margin lobed mesally. 11, Broadly hemielliptical with slightly arched ventral margin.

Van Achterberg and Salvo (1997) explicitly regarded the presence of a basal tooth as apomorphic. Thus, if the presence of a basal tooth is apomorphic, *Phaedrotoma sensu* van Achterberg and Salvo (1997) is partially defined by a symplesiomorphy. The nomenclatural changes in van Achterberg and Salvo (1997) collapse the subgeneric classification established by Fischer (1972, 1977, 1987). The species currently included in *Opius sensu lato* are segregated into the putatively monophyletic genus *Opius sensu stricto* or the seemingly paraphyletic genus *Phaedrotoma sensu lato*. Species with mandibles that are gradually widened distally to proximally (Fig. 14) cannot be unequivocally placed in either genus. Additionally, species that exhibit distinct similarities in clypeal shape, body

sculpture, and wing venation (e.g. *O. relativus* Fischer and *O. salmonensis*) fall into different genera. Because of these shortcomings I see no reason to adopt the classification proposed by van Achterberg and Salvo (1997) over Fischer (1972, 1977, 1987).

The Nearctic species of *Opius sensu lato* that fall within *Gastrosema* vary extensively in mandibular shape. In *O. lacopitaensis* Kula, new species (described below) the basal tooth is obviously absent in most individuals but gradually widened distally to proximally in some individuals. The absence of the basal tooth is the most commonly observed condition for Nearctic species in *Gastrosema*. The continuous nature of this character makes it very difficult to code into discrete character states



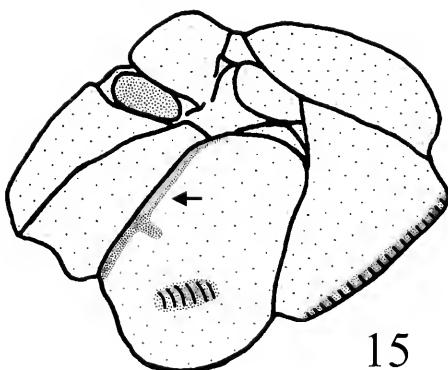
Figs. 12–14. Mandibles. 12, Basal tooth distinctly present. 13, Basal tooth completely absent. 14, Gradually widened distally to proximally.

for certain species. However, species such as *O. salmonensis* consistently lack a basal tooth, and species such as *O. relativus* consistently possess a distinct basal tooth. *Opisus tangens* Fischer is another Nearctic species in *Gastrosema* that possesses a distinct basal tooth. Unfortunately, only one individual was available for examination, so intraspecific variation of mandibular shape is not known for *O. tangens*. Nearctic species in several subgenera exhibit variation in mandibular shape similar to Nearctic species in *Gastrosema*. *Phaedrotoma sensu* Fischer (1972) and *Pleurosema* contain species that either obviously lack or distinctly possess a basal tooth, as well as species with mandibular shapes that cannot be reliably determined as basal tooth present or absent. The results from this study suggest that mandible shape is

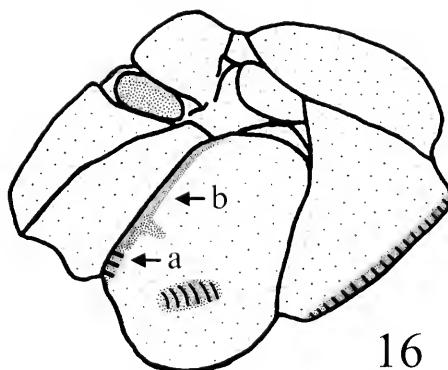
useful for distinguishing between certain species but may not be possible to code unambiguously for phylogenetic analyses.

*Sculpture associated with posterior mesopleural furrow.*—Fischer (1972) segregated species in *Opisus* into different subgenera based on the presence or absence of crenulations within the posterior mesopleural furrow. This interpretation is inadequate because within a species the posterior mesopleural furrow can be either entirely smooth or crenulate below but smooth above the episternal scrobe. Nearctic species in *Gastrosema* that exhibit this condition include *O. abbyae* Kula, new species (described below) (Figs. 15–16).

An entirely smooth posterior mesopleural furrow is found in the majority of Nearctic species in *Gastrosema*. Yet several species in *Gastrosema* consistently possess



15



16

Figs. 15–16. Posterior mesopleural furrow. 15, Entirely smooth. 16, Crenulate below (arrow a) but smooth above (arrow b) episternal scrobe. Figs. modified from Fischer (1972).

an entirely crenulate posterior mesopleural furrow (Fig. 1). *Opius flaviceps*, *O. relativus*, *O. salmonensis*, and *O. tangens* are Nearctic species in *Gastrosema* that possess an entirely crenulate posterior mesopleural furrow. Additionally, several Nearctic species in *Pleurosema* consistently possess an entirely crenulate posterior mesopleural furrow. When interpreting this character in phylogenetic analyses, the location of crenulations in the posterior mesopleural furrow is more informative than the mere presence or absence of crenulations and may be important for establishing homology.

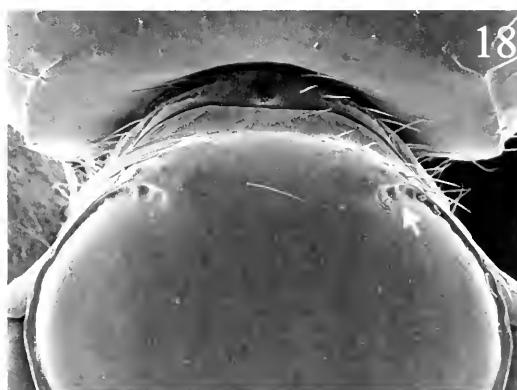
*Presence or absence of mesoscutal midpit.*—Fischer (1972) used the presence or absence of the mesoscutal midpit (Fig. 17) to divide the subgenera of *Opius* into two

roughly equal sized groups. The assessment of variation conducted in this study confirms the potential phylogenetic utility of this character. Midpit shape and depth vary intraspecifically in Opiinae, but the midpit is consistently present or absent for a particular species. All Nearctic species in *Gastrosema* consistently lack a midpit, but there are several Nearctic species in other subgenera that consistently possess a midpit. Because the midpit can be quite reduced within a species, specimens should be examined at the appropriate angle and with light dispersing plastic (mylar).

*Presence, absence, and sculpture associated with notauli.*—Species in Opiinae exhibit several character states associated with the notauli. Historically, the length of the notauli has been used to group putatively

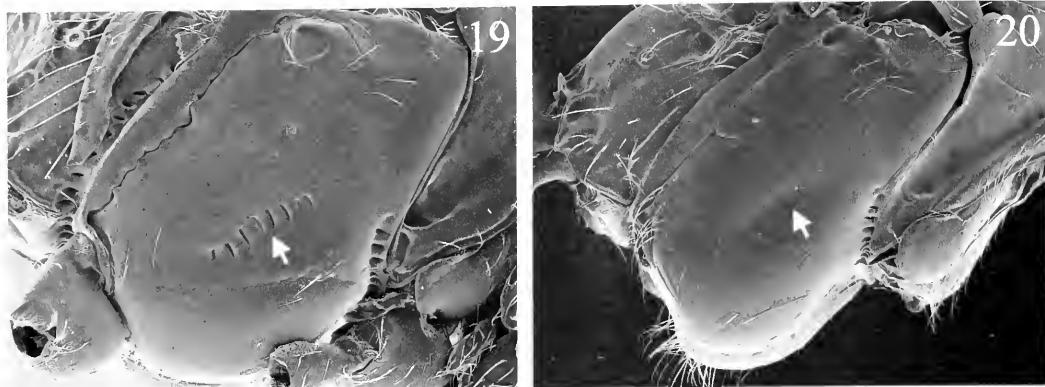


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18

Figs. 17–18. 17, Mesoscutal midpit. 18, Notauli represented by shallow anterior depressions.



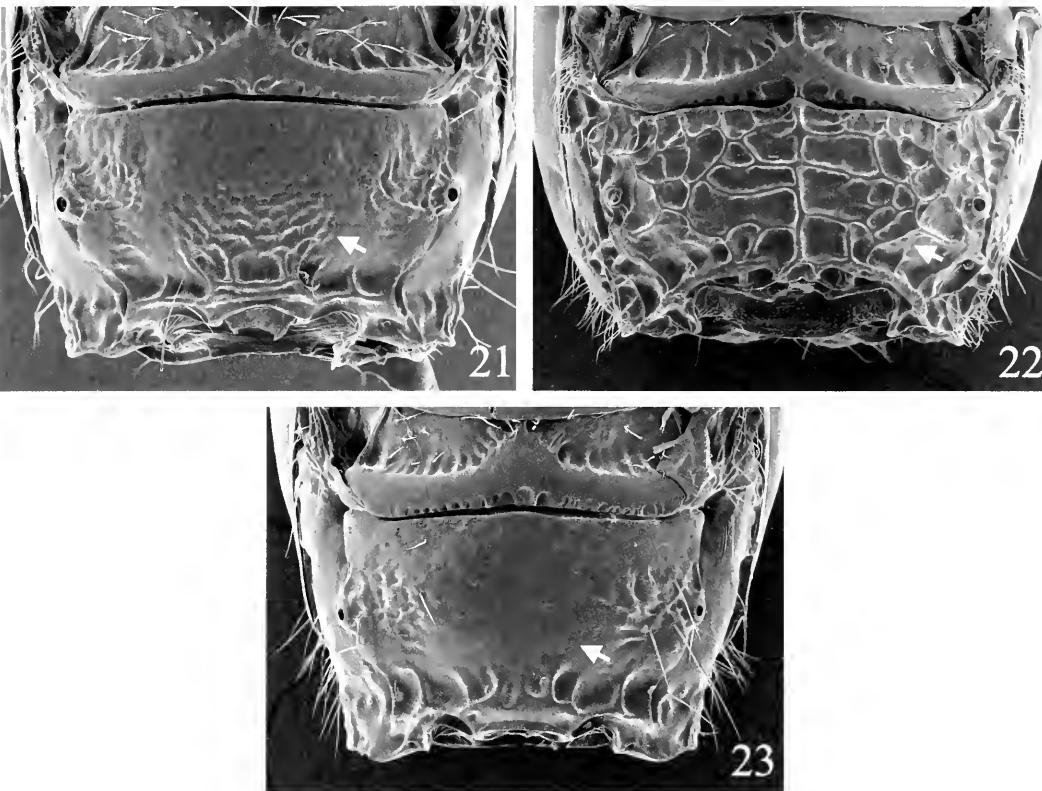
Figs. 19–20. Sternaulus. 19, Short, narrow, and crenulate. 20, Represented by a smooth depression.

closely related species (Fischer 1972). However, the presence or absence of crenulations within the notauli, as well as the termination point of the notauli, may provide additional useful information for phylogenetic inference. Among Nearctic species in *Gastrosema*, the notauli are shallow or deep anterior depressions that can be sculptured or unsculptured (Fig. 18).

*Presence, absence, and sculpture associated with sternaulus.*—Fischer (1972) used the following three attributes to partially define certain subgenera: sternaulus absent, sternaulus present and smooth, and sternaulus present and sculptured (e.g. crenulate). *Gastrosema* is partially defined by the presence of sculpture within the sternaulus. The most commonly observed condition for Nearctic species in *Gastrosema* is a relatively short and narrow sternaulus with crenulate sculpture (Fig. 19). However, examination of multiple individuals for several Nearctic species in *Gastrosema* revealed that the sternaulus can vary from a smooth depression (Fig. 20) to distinctly crenulate within a species. Species that exhibit this condition include *O. lacopitaensis* and *O. striativentris*. Further, species such as *O. castaneigaster* Fischer often possess a very weakly sculptured sternaulus that can appear unsculptured using a stereomicroscope with a fiber optic illuminator. Despite this large breadth of variation, Fischer (1972) used the presence

and absence of sculpture within the sternaulus to place species in *Gastrosema* and *Phaedrotoma*, respectively. Because the presence and absence of sculpture within the sternaulus can vary intraspecifically, certain Nearctic species in *Phaedrotoma sensu* Fischer (1972) potentially share a most recent common ancestor with certain Nearctic species in *Gastrosema*. The high level of intraspecific variation in sternaulus sculpture limits the use of this character in phylogenetic analyses. If sculpture within the sternaulus is utilized in future phylogenetic analyses, the location of the sternaulus and the type of sculpture within the sternaulus are important for establishing homology.

*Sculpture associated with propodeum.*—The presence or absence of propodeal sculpture is a major defining feature for several subgenera in *Opis*. In Fischer (1972) the presence or absence of propodeal sculpture is the only attribute differentiating species in *Merotrachys* and *Phaedrotoma*, respectively. The presence, absence, and type of propodeal sculpture are quite variable among Nearctic species in *Gastrosema*, but these attributes are only slightly variable within a species. For example, in *O. striativentris* the propodeum is rugulose to rugose (Fig. 21), in *O. intermissus* Fischer the propodeum is always rugose, and in *O. salmonensis* the propodeum is always areolate-rugose (Fig. 22).



Figs. 21–23. Propodeal sculpture. 21, Rugulose. 22, Areolate-rugose. 23, Smooth with rugulose sculpture surrounding spiracles.

The majority of Nearctic species in *Gastrosema* possess a rugulose to rugose propodeum. However, species that possess an areolate-rugose propodeum are also commonly encountered. Further, species with an areolate-rugose propodeum usually have an entirely crenulate posterior mesopleural furrow. Nearctic species that exhibit this condition include *O. flaviceps*, *O. relativis*, *O. salmonensis*, and *O. tangens*. The majority of Nearctic species in *Plenrosema* also possess an areolate-rugose propodeum and an entirely crenulate posterior mesopleural furrow. Thus, certain Nearctic species in *Pleurosema* potentially share a most recent common ancestor with certain Nearctic species in *Gastrosema*. Of the described Nearctic species in *Gastrosema*, only *O. hancockianus* Fischer has a nearly entirely smooth propodeum (Fig.

23). A trace of rugulose sculpturing surrounds the propodeal spiracles, but the rest of the propodeum is completely smooth. This condition is also commonly observed for Nearctic species in *Phaedrotoma sensu* Fischer (1972).

Propodeal sculpture can be assigned distinct character states, and different types of propodeal sculpture often correlate with sculpture in the posterior mesopleural furrow. Species with an areolate-rugose propodeum frequently have an entirely crenulate posterior mesopleural furrow, and species with a smooth or rugulose to rugose propodeum typically do not have an entirely crenulate posterior mesopleural furrow. Consideration of propodeal sculpture in phylogenetic analyses must go beyond the presence or absence of sculpture. Different types of propodeal

sculpture, and the correlation between propodeal sculpture and sculpture associated with other anatomical features, should be considered.

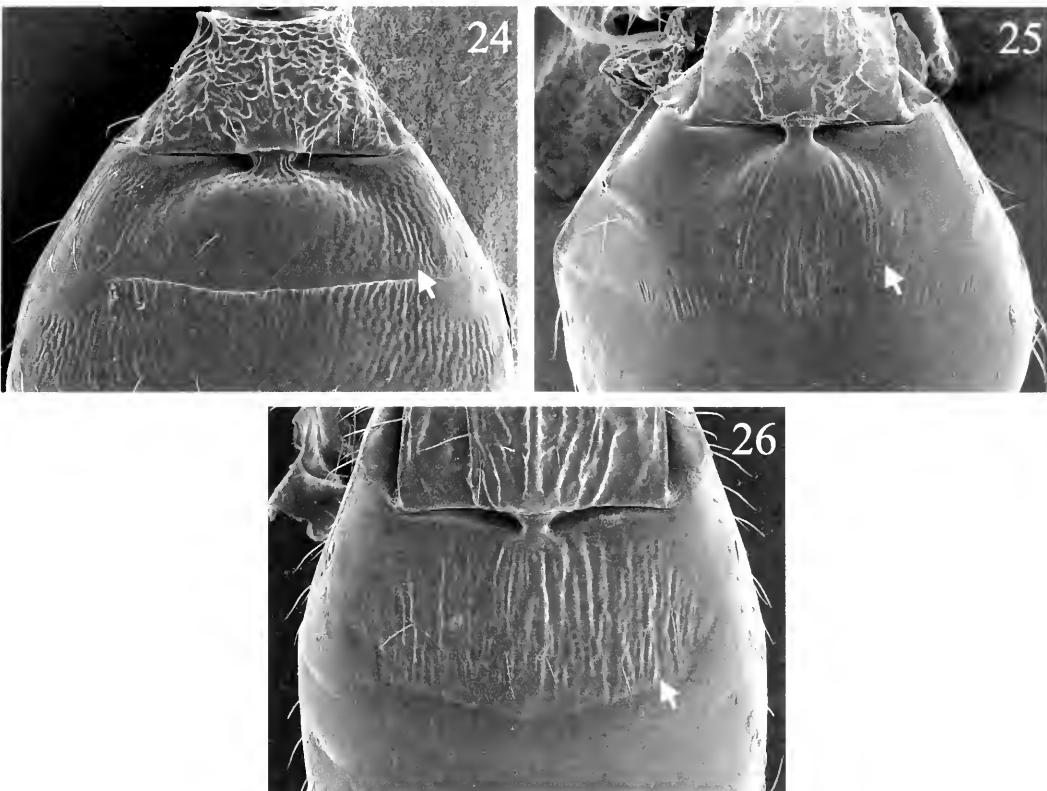
*Sculpture associated with median abdominal tergites.*—In Fischer's original diagnosis for *Gastrosema*, a major defining feature was the presence of "shagreened" or coriaceous sculpture on abdominal tergite two (t2) (Fig. 24) (Fischer 1972). Examination of the Nearctic species in *Gastrosema* treated by Fischer (1977) revealed that *Gastrosema* was not limited to species with a coriaceous t2. Rather, species with a carinate or costate t2 were included as well (Figs. 25–26). The vast majority of Nearctic species included in *Gastrosema* have a coriaceous t2. Examples include *O. abbyae*, *O. castaneigaster*, *O. intermissus*, *O. lacopitaensis*, and *O. striativentris*. *Opius flaviceps* and *O. salmonensis* are two species that possess a costate t2, and *O. oscinidis* possesses a carinate t2. Neither costate nor carinate sculpture on t2 is common among Nearctic species in *Gastrosema*, but a carinate t2 is commonly observed for several Nearctic species in *Rhogadopsis* *sensu* Wharton (1987) and *Thoracosema*. In terms of intraspecific variation, species with a coriaceous t2 show little variation in sculpture density. Conversely, species with a carinate or costate t2 exhibit substantial intraspecific variation in sculpture density. In *O. oscinidis* the carinations are extremely reduced in some individuals, and t2 appears smooth unless the specimens are examined at several angles using mylar and a variety of light intensities. Yet the carinations on t2 are unmistakably present in other individuals. Thus, sculpture on t2 has potential phylogenetic importance but may be difficult to code unambiguously for certain species.

*Configuration of forewing venation.*—Fischer (1972) used the position of vein 1m-cu relative to vein 2RS to segregate species into certain subgenera. For example, species that Fischer placed in *Phlebosema* Fischer possess vein 1m-cu basad or directly

in line with vein 2RS (Figs. 27–28). *Phlebosema* is currently a junior synonym of *Baeocentrum* Schulz, but this nomenclatural change does not alter Fischer's concept of *Phlebosema* (Wharton 1987). Alternatively, species that Fischer placed in *Gastrosema* possess vein 1m-cu distad vein 2RS (Fig. 29). The results of this study confirm that species with vein 1m-cu basad vein 2RS occasionally display vein 1m-cu directly in line with vein 2RS. Further, species with vein 1m-cu distad vein 2RS never exhibit vein 1m-cu directly in line with or basad vein 2RS. All described Nearctic species in *Gastrosema* have vein 1m-cu distad vein 2RS. However, the Nearctic species in *Baeocentrum* *sensu* Wharton (1987) and certain Nearctic species in *Merotrachys* and *Tolbia* *sensu* Fischer (1972) have vein 1m-cu basad or directly in line with vein 2RS. Thus, the position of vein 1m-cu relative to vein 2RS should be evaluated in future phylogenetic analyses.

The size and shape of the forewing stigma is another character of potential phylogenetic importance. The Nearctic species in *Gastrosema* exhibit minimal intraspecific variation in stigma size and shape, but stigma size and shape can vary substantially from species to species. Several Nearctic species in *Gastrosema* exhibit conspicuous similarities in stigma size and shape. *Opius abbyae*, *O. castaneigaster*, *O. intermissus*, *O. lacopitaensis*, and *O. striativentris* possess a narrow and elongate stigma (Fig. 28), while *O. flaviceps*, *O. relativus*, *O. salmonensis*, and *O. tangens* possess a wedge shaped stigma (Fig. 29). In future studies stigma size and shape should be thoroughly examined for species in other opiine subgenera.

*Color.*—In Opiinae color is not of any apparent phylogenetic importance but is useful for distinguishing between morphologically similar species. For example, *O. intermissus* and *O. niobe* Fischer are similar in size and shape but have conspicuously different coloration on the head and mesosoma. Species such as *O. striativentris*



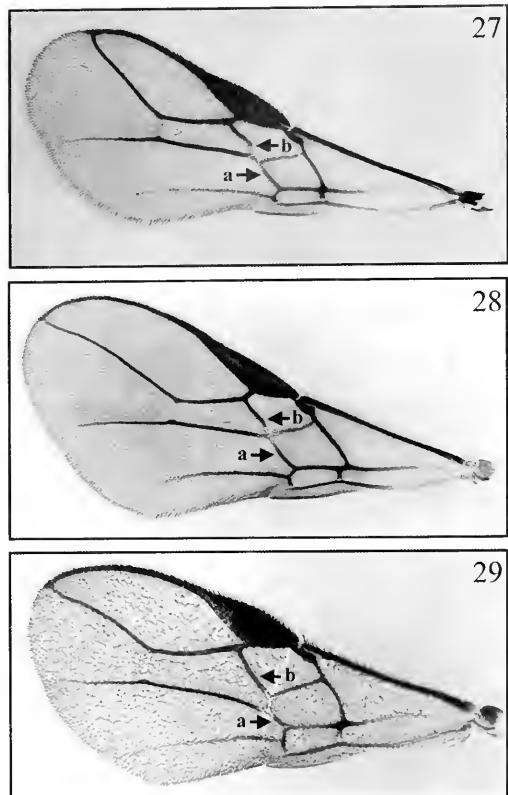
Figs. 24–26. Sculpture on t2. 24, Coriaceous. 25, Carinate. 26, Costate.

are variable in color, while color is more conserved in species such as *O. abbyae*. Thus, it is important to examine several individuals to determine the entire spectrum of color within a species. Proper specimen preparation is essential for preserving natural coloration. Specimens exposed to light for prolonged periods of time become lighter, and air-dried specimens tend to darken. Material preserved in alcohol for extended periods of time should be stored at low temperatures and protected from direct exposure to light. Specimens should be dehydrated using a critical-point-dryer or chemicals such as amyl acetate and Hexamethyl-Disilazane.

**Setation.**—Setation is another useful character for distinguishing between morphologically similar species. For example, a species of *Opium* near *extiratus* Fischer possesses a consistently setose propo-

deum, while setation on the propodeum of *O. striativentris* is usually setiferous and rarely glabrous. *Opium* near *extiratus* and *O. striativentris* are sympatric and have been reared from the same host species on the same host plant. The density of setae on the propodeum is one character that can be used to distinguish these species.

**Flagellomere number.**—Godfray (1984) demonstrated that in the alysiine *Exotela cyclogaster* Förster flagellomere number increases with body size. Alysiinae and Opiinae form a monophyletic group (Wharton 1988), and it is possible that species in Opiinae also exhibit this trend. Flagellomere number is useful when morphologically similar species have non-overlapping ranges of flagellomere number. For example, *O. abbyae* and *O. intermissus* are morphologically similar, but *O. abbyae* has 19–22 flagellomeres compared to 26–29 in



Figs. 27–29. Position of forewing vein 1m-cu (arrow a) relative to vein 2RS (arrow b). 27, 1m-cu basad 2RS. 28, 1m-cu directly in line with 2RS. 29, 1m-cu distad 2RS.

*O. intermissus*. When using flagellomere number to distinguish between species, it is important to examine several individuals to establish minimum and maximum flagellomere numbers for each species.

**Quantitative characters.**—Fischer (1972, 1977, 1987) extensively used quantitative ratios in keys to subgenera, species groups, and species in *Opius*, but the ratios were based on measurements of one or a few individuals. As a result most taxa treated in the keys cannot be reliably identified. A prime example is the treatment of species groups in Fischer's (1977) key to New World *Gastrosema*. The defining character of the *lissopleurum*-group of species is "thorax 1.25–1.40× as long as high." *Opius intermissus* is included in the *liso-*

*pleurum*-group, but the results of this study indicate that the thorax is 1.12–1.30× as long as high in *O. intermissus*. Only 33.0% of the specimens examined for *O. intermissus* fit within the morphological limits of the *lissopleurum*-group as defined by Fischer (1977).

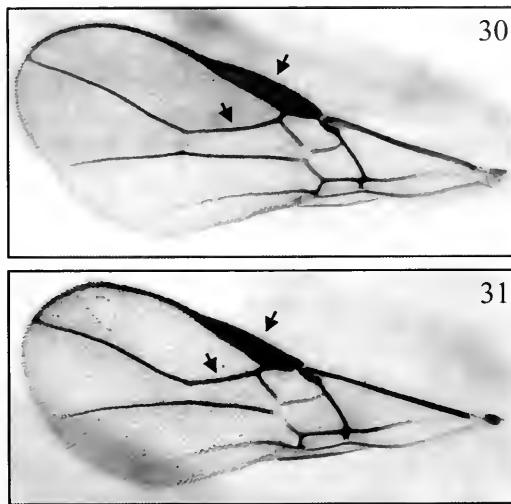
Another problem with the use of quantitative ratios is that measurement error as high as 15.7% can occur when the same specimen is measured on different dates. Factors that contribute to measurement error may be found in Wharton (1980). Given the limitations of quantitative characters, it is preferable to use qualitative characters in phylogenetic analyses and identification systems. However, measurements can be useful for distinguishing certain species. *Opius flaviceps* and *O. salmonensis* are similar in terms of coloration and sculpture, but the two species can be differentiated using ovipositor length, mesosoma length, and mesosoma width. When using measurements to characterize a species, it is optimal to measure several individuals to establish the entire range of variation for each measurement. In cases where only one or a few individuals are available for examination, the taxonomist should consider the usefulness of quantitatively describing the species.

#### NEARCTIC SPECIES IN THE SUBGENUS *GASTROSEMA*

**Species group diagnoses.**—With the exception of *O. walleyi*, all described Nearctic species in *Gastrosema* fall into three easily characterized groups that have not been recognized in previous studies (Table 1). A diagnosis of each group is provided to facilitate future studies examining the monophyly and relationships of species in *Opius*. Each group should be viewed as a hypothesis supported by potentially phylogenetically informative characters, and the monophyly of each group will be tested in future phylogenetic analyses. The first three characters presented in each di-

Table 1. Placement of described Nearctic species in *Gastrosema* into three previously unrecognized species groups.

flaviceps-group	oscinidis-group	striativentris-group
<i>flaviceps</i>	<i>oscinidis</i>	<i>abbyae</i>
<i>relativus</i>		<i>adductus</i>
<i>salmonensis</i>		<i>alconanus</i> Fischer
<i>tangens</i>		<i>castaneigaster</i>
		<i>clevelandensis</i>
		<i>cordobensis</i>
		<i>deiphobe</i> Fischer
		<i>hancockanus</i>
		<i>intermissus</i>
		<i>lacopitaensis</i>
		<i>niobe</i>
		<i>pallas</i>
		<i>porteri</i> Fischer
		<i>striativentris</i>



Figs. 30-31. Shape of forewing stigma and second submarginal cell. 30, *oscinidis*-group. 31, *striativentris*-group.

agnosis differentiate each group from the remaining *Opisus* *sensu lato*.

*flaviceps*-group: midpit absent; clypeus reduced, labrum exposed when mandibles closed; 1m-cu distad 2RS; posterior mesopleural furrow crenulate above episternal scrobe; propodeum rugose to areolate-rugose; abdominal tergites posterior to t1 smooth or variously sculptured; forewing stigma usually broad and wedge shaped, second submarginal cell size and shape variable but often shaped as in Fig. 29.

*oscinidis*-group: midpit absent; clypeus reduced, labrum exposed when mandibles closed; 1m-cu distad 2RS; posterior mesopleural furrow smooth above episternal scrobe; propodeum smooth to rugose; abdominal tergites posterior to t1 smooth or longitudinally carinate; forewing stigma usually narrow and elongate, second submarginal cell long and usually shaped as in Fig. 30.

*striativentris*-group: midpit absent; clypeus reduced, labrum exposed when mandibles closed; 1m-cu distad 2RS; posterior mesopleural furrow smooth above episternal scrobe; propodeum smooth to rugose; at least one abdominal tergite posterior to t1 coriaceous; forewing stigma usually

narrow and elongate, second submarginal cell short and usually shaped as in Fig. 31.

*Discussion.*—The posterior mesopleural furrow in *O. walleyi* is smooth above the episternal scrobe, and thus, *O. walleyi* does not fall within the *flaviceps*-group. The shape of the second submarginal cell in *O. walleyi* fits the diagnosis for the *oscinidis*-group. However, t2 and t3 are coriaceous which fits the diagnosis for the *striativentris*-group. Thus, *Opisus walleyi* possesses characteristics of both the *oscinidis*-group and the *striativentris*-group and is left unplaced at this time.

*Opisus pumilio* (the type species for *Gastrosema*) belongs in the *striativentris*-group. Additionally, several Nearctic species treated in Fischer (1977) were not included in *Gastrosema* but belong in one of the three species groups (Table 2). Thus, if the species groups proposed in this study are monophyletic, subgenera with species that fall within the species groups are obviously not monophyletic.

In future studies of *Opisus*, species in *Allophlebus* Fischer, *Gastrosema*, *Hypocynodus* Förster *sensu* Fischer (1972), *Merotrachys*, *Opiothorax* Fischer, *Pendopius* Fischer, *Phaedrotoma* *sensu* Fischer (1972), *Pleurose-*

Table 2. Placement of described Nearctic species not included in *Gastrosema* into three previously unrecognized species groups.

flaviceps-group	oscinidis-group	striativentris-group
<i>O. (Pleurosema)</i>	<i>O. (Rhogadopsis)</i>	<i>O. (Merotrachys)</i>
<i>euwattacoanum</i> Fischer	<i>stenopectus</i> Fischer	<i>brownsvilleensis</i> Fischer
<i>hermosanus</i> Fischer	<i>(Thoracosema)</i>	<i>lansingensis</i> Fischer
<i>metatensis</i> Fischer	<i>crabtreeanus</i> Fischer	<i>paulior</i> Fischer
<i>orizabensis</i> Fischer	<i>extiratus</i>	<i>paulus</i> Fischer
<i>paratakomanus</i> Fischer	<i>parkercreekensis</i> Fischer	<i>virentis</i> Fischer
<i>pilosinotum</i> Fischer	<i>prolongatus</i> Fischer	<i>O. (Phaedrotoma)</i>
<i>sybile</i> Fischer	<i>pseudocolumbiacus</i> Fischer	<i>complicans</i> Fischer
<i>thalis</i> Fischer	<i>schnieri</i> Fischer	<i>O. (Tolbia)</i>
<i>O. (Rhogadopsis)</i>	<i>southcarolinensis</i> Fischer	<i>heroicus</i> Fischer
<i>northcarolinensis</i> Fischer		

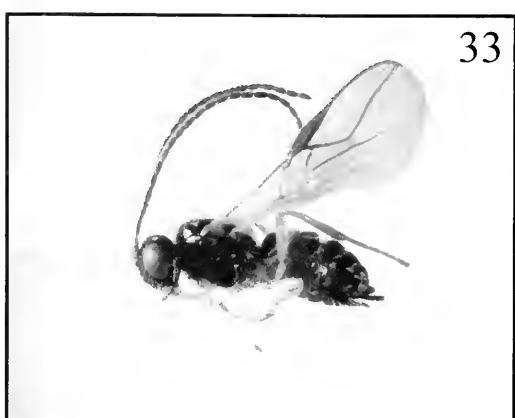
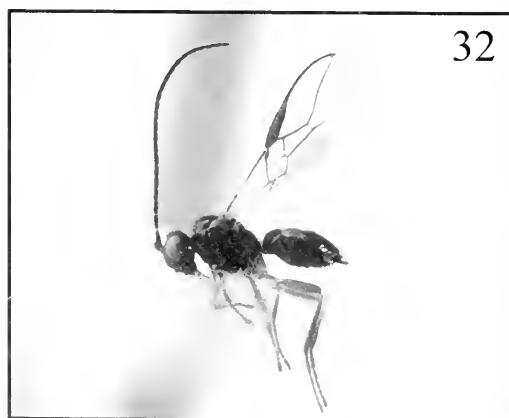
*ma*, *Rhogadopsis* *sensu* Wharton (1987), *Thoracosema*, and *Tolbia* *sensu* Fischer (1972) should be examined to determine which species group, if any, they fit into. Examination of species in the aforementioned subgenera will almost certainly result in the discovery of species groups in addition to the three discovered during this research. Placement of all described species in these subgenera will be a monumental task, as several hundred holotypes must be examined. The holotypes are housed in repositories found throughout the world, although most are in North American and European museums and collections. Species currently included in subgenera not listed above lack at least one of the three characters used to differ-

entiate the three species groups from the remaining *Opius* *sensu lato* (see species group diagnoses).

*Opius (Gastrosema) abbyae* Kula,  
new species

Fig. 32

*Female*.—*Head*: 1.23–1.36× as wide as long; eyes 0.67–0.77× as wide as long, glabrous; face smooth with rugulose sculpture between antennal sockets and compound eyes, slightly raised mesally, setiferous; clypeus hemielliptical, convex, ventral margin straight, setiferous; mandibles simple, with two apical teeth per mandible, setiferous; antennae with 19–21 flagellomeres. *Mesosoma*: 0.30–0.40 mm wide; 0.51–0.64 mm long; 0.58–0.66× as



Figs. 32–33. *Opius* spp. 32, *O. abbyae*. 33, *O. lacopitaensis*.

wide as long;  $0.71\text{--}0.81\times$  as wide as deep;  $1.10\text{--}1.31\times$  as long as deep; pronotum coriaceous laterally, crenulate in anterior furrow; notauli represented by anterior depressions; mesoscutum smooth, setiferous (78.6%) or sparsely setiferous anteriorly and along lines where notauli would run if present (21.4%); mesopleuron nearly entirely smooth, usually rugulose or crenulate near tegulae (85.8%), rarely smooth near tegulae (14.2%), sternaulus distinctly crenulate; scutellar disc smooth; propodeum rugose, setiferous; metapleuron setiferous. *Metasoma*: t1  $0.93\text{--}1.25\times$  as wide as long, rugulose to rugose; t2 coriaceous; t3 coriaceous; t4 always at least partially coriaceous; remaining tergites smooth; exposed ovipositor  $0.11\text{--}0.26$  mm long. *Legs*: smooth, setiferous, hind tibia  $0.95\text{--}1.09\times$  as long as mesosoma length. *Wings*: hyaline; forewing stigma narrow and elongate; 2RS  $0.53\text{--}0.71\times$  as long as 3RSa; 2RS  $0.41\text{--}0.50\times$  as long as 2M; 3RSa  $0.70\text{--}0.77\times$  as long as 2M. *Color*: head entirely very dark brown to black; mesosoma usually black (85.7%), rarely very dark brown (14.3%); t1 entirely dark brown to nearly entirely dark brown with slight brownish orange coloration laterally; t2 light brown to dark brown medially, orange to yellow laterally; t3 usually brown to dark brown with orange to yellow coloration at antero-lateral edges (85.7%), rarely entirely dark brown (14.3%); t4 usually entirely dark brown (92.9%), rarely brownish yellow (7.1%); remaining tergites dark brown; legs yellow to yellowish brown, prothoracic legs lighter than mesothoracic legs, mesothoracic legs lighter than metathoracic legs, metatibia and metatarsus always yellowish brown.

*Male*.—As in ♀ except: *Head*:  $1.21\text{--}1.30\times$  as wide as long; eyes  $0.64\text{--}0.71\times$  as wide as long; antennae with 20–22 flagellomeres. *Mesosoma*:  $0.57\text{--}0.61\times$  as wide as long;  $1.24\text{--}1.32\times$  as long as deep. *Wings*: 2RS  $0.50\text{--}0.53\times$  as long as 2M. *Color*: mesosoma always black.

*Host*.—*Calycomyza* sp. mining the leaves of *Helianthus annuus* (TAMU).

*Material examined*.—Holotype ♀: USA, Nebraska, Arthur County, Highway 61 south of Arthur near Arapaho Prairie, 8.vii.1999, R. R. Kula and A. A. Rogers (TAMU). Paratypes: 6♀, same data as holotype; 2♀, 1♂, same data as holotype except 11.vii.1998; 5♀, 3♂, same data as holotype except 10.vii.1999 (TAMU).

*Diagnosis*.—Within the *striativentris*-group *O. intermissus*, *O. lacopitaensis*, and *O. weemsi* Fischer are morphologically similar to *O. abbyae*. Head coloration can be used to distinguish *abbyae* from both *intermissus* and *weemsi*. In *abbyae* the head is entirely very dark brown to black. Alternatively, in *intermissus* the head is yellow with the vertex very dark brown to black, and in *weemsi* the head is mostly orange with the vertex very dark brown and the ventral half of the face brown. The number of antennal flagellomeres can also be used to distinguish *abbyae* from *intermissus* and *weemsi*. *Opius abbyae* possesses 19–22 flagellomeres, while *intermissus* possesses 26–29 flagellomeres and *weemsi* possesses 32 flagellomeres. Another character that can be used to differentiate *abbyae* from *intermissus* and *weemsi* is tergite coloration. Tergite 3 in *abbyae* is usually brown to dark brown with orange to yellow coloration at the antero-lateral edges. In *intermissus* t3 is yellow with the posterior edge dark brown, and in *weemsi* t3 is orangish yellow with the posterior edge dark brown. Sculpture on the abdominal tergites can be used to distinguish *abbyae* from *lacopitaensis*. In *abbyae* t4 is always coriaceous, while in *lacopitaensis* t4 is never coriaceous.

*Discussion*.—*Opius abbyae* falls within the *striativentris*-group. This species exhibits less intraspecific variation in qualitative characters than observed for *intermissus*, *lacopitaensis*, *oscinidis*, and *striativentris*. For example, the sternaulus is consistently crenulate in *abbyae*, while the sternaulus varies from a smooth depression to cren-

ulate in *lacopitaensis* and *striativentris*. Coloration of the head and mesosoma is much less variable in *abbyae* than in *oscinidis* or *striativentris*. No substantial differences were observed between female and male specimens in *abbyae*.

**Etymology.**—This species is named in honor of Abigail Rogers Kula who assisted in collection of the host.

***Opius (Gastrosema) lacopitaensis* Kula,  
new species**

Fig. 33

**Female.**—*Head*: 1.25–1.36× as wide as long; eyes 0.67–0.73× as wide as long, glabrous; face usually smooth with rugulose sculpture between antennal sockets and compound eyes (92.9%), rarely minutely coriaceous with rugulose sculpture between antennal sockets and compound eyes (7.1%), slightly raised mesally, setiferous; clypeus narrowly hemielliptical to crescent shaped, convex, ventral margin straight to slightly arched, setiferous; mandibles simple to gradually widened distally to proximally, with two apical teeth per mandible, setiferous; antennae with 19–20 flagellomeres. *Mesosoma*: 0.29–0.35 mm wide; 0.51–0.61 mm long; 0.55–0.64× as wide as long; 0.69–0.75× as wide as deep; 1.14–1.27× as long as deep; pronotum often entirely coriaceous laterally (78.6%), occasionally smooth dorsally and coriaceous ventrally (21.4%), crenulate in anterior furrow; notaui represented by anterior depressions; mesoscutum smooth, setiferous anteriorly and along lines where notaui would run if present; mesopleuron nearly entirely smooth, often smooth near tegulae (78.6%), occasionally crenulate near tegulae (21.4%), sternaulus often crenulate (78.6%), occasionally a smooth depression (21.4%); scutellar disc smooth; propodeum rugose, setiferous; metapleuron setiferous. *Metasoma*: t1 0.71–1.00× as wide as long, rugose; t2 coriaceous; t3 coriaceous; remaining tergites smooth; exposed ovipositor 0.16–0.32 mm long. *Legs*: smooth, setiferous, hind tibia 0.88–0.97× as long as mesosoma length.

*Wings*: hyaline; forewing stigma narrow and elongate; 2RS 0.56–0.64× as long as 3RSa; 2RS 0.41–0.48× as long as 2M; 3RSa 0.67–0.77× as long as 2M. *Color*: head entirely dark brown to very dark brown; mesosoma entirely dark brown to very dark brown; t1 dark brown; t2 brownish orange to yellow; t3 anterior half to two thirds brownish orange to yellow, posterior half to one third brown; remaining tergites brown to dark brown; legs yellow, posterior portion of metatibia and entire metatarsus yellowish brown.

*Male*.—As in ♀ except: *Head*: eyes 0.67–0.79× as wide as long; face usually smooth with rugulose sculpture between antennal sockets and compound eyes (90.9%), rarely entirely smooth (9.1%); antennae with 19–22 flagellomeres. *Mesosoma*: 0.54–0.67 mm long; 0.68–0.73× as wide as deep; 1.17–1.38× as long as deep; pronotum often coriaceous laterally (63.6%), occasionally smooth (36.4%); mesopleuron nearly entirely smooth, usually smooth near tegulae (90.9%), rarely crenulate near tegulae (9.1%), sternaulus often a smooth depression (54.6%), occasionally crenulate (45.5%). *Wings*: 2RS 0.56–0.67× as long as 3RSa.

*Host*.—Unknown.

*Material examined*.—Holotype ♀: USA, Texas, Jim Wells County, 8 miles west of Ben Bolt, La Copita Research Station, 20.v.1987, J. B. Woolley (TAMU). Paratypes: 11♀, 11♂, same data as holotype; 2♀, same data as holotype except northwest of Ben Bolt, 21.v.1987, G. Zolnerowich (TAMU).

*Diagnosis*.—Within the *striativentris*-group *O. abbyae*, *O. castaneigaster*, *O. cordobensis* Fischer, and *O. pallas* Fischer are morphologically similar to *O. lacopitaensis*. Characters used to differentiate *lacopitaensis* from *abbyae* and *castaneigaster* can be found in the diagnoses for *abbyae* and *castaneigaster*. *Opium lacopitaensis* can be differentiated from *cordobensis* using propodeal sculpture. In *lacopitaensis* the propodeum is rugulose to rugose, while in *cor-*

*dobensis* the propodeum is very heavily rugose with conspicuous carinae throughout. The number of antennal flagellomeres can be used to distinguish *lacopitaensis* from *pallas*. *Opius lacopitaensis* possesses 19–22 flagellomeres, while *pallas* possesses 28 flagellomeres.

**Discussion.**—*O. lacopitaensis* falls within the *striativentris*-group. In Fischer's subgeneric classification individuals with a crenulate sternaulus fall within *Gastrosema*, but individuals with a smooth sternaulus fall within *Merotrachys*. *Opius lacopitaensis* is provisionally placed in *Gastrosema* because the majority of individuals (i.e. 16 of 25) fall within *Gastrosema*.

*Opius lacopitaensis* exhibits variation in color and sculpture similar to that observed in *castaneigaster*. No substantial differences were observed between female and male specimens in *lacopitaensis*. No biological data are associated with *lacopitaensis*, but other species in the *striativentris*-group have been reared from leaf mining Agromyzidae (e.g. *O. abbyae*, *O. adductus* Fischer, *O. striativentris*).

**Etymology.**—This species is named after the collection site.

***Opius (Gastrosema) castaneigaster***  
Fischer

*Opius castaneigaster* Fischer 1964: 413, 419.

*Opius (Gastrosema) castaneigaster*: Fischer 1977: 311, 324.

**Female.**—*Head*: 1.19–1.33× as wide as long; eyes 0.62–0.75× as wide as long, glabrous; face usually smooth with rugulose sculpture between antennal sockets and compound eyes (91.7%), rarely entirely smooth (8.3%), slightly raised mesally, setiferous; clypeus hemispherical, convex, ventral margin straight, setiferous; mandibles simple, with two apical teeth per mandible, setiferous; antennae with 21–24 flagellomeres. *Mesosoma*: 0.30–0.45 mm wide; 0.54–0.82 mm long; 0.53–0.64× as wide as long; 0.79–0.93× as wide as deep; 1.29–1.70× as long as deep; pronotum co-

riaceous laterally, crenulate in anterior furrow; notauli represented by anterior depressions; mesoscutum smooth, setiferous anteriorly and along lines where notauli would run if present; mesopleuron nearly entirely smooth, usually rugulose or crenulate near tegulae (91.7%), rarely smooth near tegulae (8.3%), sternaulus usually crenulate (91.7%), rarely reduced to a sculptured depression (8.3%); scutellar disc smooth; propodeum rugulose to rugose, setiferous; metapleuron sparsely setiferous to setiferous. *Metasoma*: t1 1.00–1.33× as wide as long, rugulose to rugose; t2 usually coriaceous (91.7%), rarely smooth (8.3%); t3 usually at least partially coriaceous (91.7%), rarely entirely smooth (8.3%); remaining tergites smooth; exposed ovipositor 0.24–0.49 mm long. *Legs*: smooth, setiferous, hind tibia 0.83–0.95× as long as mesosoma length. *Wings*: hyaline; forewing stigma narrow and elongate; 2RS 0.48–0.67× as long as 3RSa; 2RS 0.39–0.50× as long as 2M; 3RSa 0.73–0.84× as long as 2M. *Color*: head entirely brown to dark brown; mesosoma entirely brown to dark brown; t1 brown to dark brown; t2 orange to yellow; t3 anterior half orange to yellow, posterior half brown to dark brown or t3 anterior two thirds orange to yellow, posterior one third brown to dark brown; remaining tergites dark brown; legs orangish yellow to yellow, metatibia and metatarsus usually yellowish brown (83.3%).

**Male.**—As in ♀ except: *Head*: 1.11–1.26× as wide as long. *Mesosoma*: 0.51–0.60× as wide as long. *Metasoma*: t1 0.86–1.17× as wide as long.

**Host.**—Unknown.

**Material examined.**—Holotype ♀: USA, New York, Tompkins County, Ithaca, 7.ix.1935, H. K. Townes (AEI). Allotype ♂: same data as holotype except 1.vi.1935 (AEI). Paratypes: all USA; 1♀, same data as holotype except 30.v.1934; 1♂, New York, Oneida County, Rome, 24.vi.1934, H. K. Townes; 1♀, New York, Delaware County, Hancock, 31.vii.1935, H. K.

Townes; 1♀, 1♂, New York, Otsego County, Oneonta, 17.viii.1935, H. K. Townes; 1♀, New York, Otsego County, Oneonta swamp, 1,900 feet elevation, 18.viii.1935, H. K. Townes; 1♀, Ohio, Summit County, Akron, 18.v.1941, H. K. Townes; 1♀, South Carolina, Greenville County, Greenville, 22.iv.1952, G. and L. Townes; 1♀, South Carolina, Greenville County, Greenville, 31.v.1952, G. and L. Townes; 1♀, South Carolina, Pickens County, Wattacoo, 10.v.1959, G. F. Townes; 1♂, South Carolina, Pickens County, Wattacoo, 6.v.1961, G. F. Townes; 1♀, South Carolina, Pickens County, Wattacoo, 19.v.1961, G. F. Townes (AEI); 1♀, Wisconsin, Polk County, July, collection C. F. Baker (USNM). Other determined material: 1♀, same data as holotype (det. Fischer) (AEI).

**Diagnosis.**—Within the *striativentris*-group, *O. cordobensis*, *O. lacopitaensis*, *O. niobe*, *O. pallas*, and *O. striativentris* are morphologically similar to *O. castaneigaster*. Propodeal sculpture can be used to distinguish *castaneigaster* from *cordobensis*. In *castaneigaster* the propodeum is rugulose to rugose, while in *cordobensis* the propodeum is very heavily rugose with conspicuous carinae throughout. *Opius castaneigaster* can be differentiated from *niobe* on the basis of mesosoma shape and the number of antennal flagellomeres. In *castaneigaster* the mesosoma is subelliptical (1.29–1.70× as long as deep), and the number of flagellomeres ranges from 21–24. In *niobe* the mesosoma is subspherical (1.21–1.23× as long as deep), and the number of flagellomeres ranges from 25–31. *Opius pallas* is very morphologically similar to *castaneigaster*, but the two species can be differentiated using flagellomere number. *Opius pallas* possesses 28 flagellomeres, while the maximum number of flagellomeres for *castaneigaster* is 24. Several characters can be used to distinguish *castaneigaster* from *striativentris*. Tergite 1 is brown to dark brown in *castaneigaster*, while t1 is usually yellow to brownish orange in *striativentris*. Tergite 3 is only

partially coriaceous in *castaneigaster*, as opposed to entirely coriaceous in *striativentris*. Tergite 4 is always smooth in *castaneigaster*, while t4 is smooth or coriaceous in *striativentris*. The mesosoma is uniformly brown or dark brown in *castaneigaster*, while the mesonotum is often conspicuously darker than the rest of the mesosoma in *striativentris*. *Opius castaneigaster* can be differentiated from *lacopitaensis* using t1 width to length ratios, clypeus shape, and the number of flagellomeres. Tergite 1 width in *castaneigaster* is usually greater than or equal to t1 length (91.7%) and is rarely less than t1 length (8.3%). Tergite 1 width in *lacopitaensis* is always less than or equal to t1 length. The shape of the clypeus is hemispherical in *castaneigaster*, while the shape of the clypeus is narrowly hemielliptical to crescent shaped in *lacopitaensis*. *Opius castaneigaster* possesses 21–24 flagellomeres, as opposed 19–22 in *lacopitaensis*.

**Discussion.**—*Opius castaneigaster* falls within the *striativentris*-group. *Opius pallas* may eventually be determined as a synonym of *castaneigaster*. The two species are very morphologically similar and exhibit overlapping geographic distributions. *Opius pallas* is only known from the holotype, and acquisition of additional specimens may reveal a broader range of flagellomere number.

One specimen of *castaneigaster* examined in this study lacks sculpture on t2 and t3. However, no additional attributes were observed that indicated the specimen was not *castaneigaster*. Single specimens with reduced sculpture are very difficult to identify, and comparison of these individuals with a long series of determined specimens will facilitate their identification. No biological data are associated with *castaneigaster*, but other species in the *striativentris*-group have been reared from leaf mining Agromyzidae (e.g. *O. abyae*, *O. adductus*, *O. striativentris*).

***Opius (Gastrosema) intermissus* Fischer***Opius intermissus* Fischer 1964: 413, 428.*Opius (Gastrosema) intermissus*: Fischer 1977: 314, 357.

**Female.**—*Head*: 1.23–1.29× as wide as long; eyes 0.62–0.67× as wide as long, glabrous; face minutely coriaceous with rugulose sculpture between antennal sockets and compound eyes, slightly raised mesally, usually setose (80.0%), rarely setiferous (20.0%); clypeus hemispherical, convex, ventral margin straight, usually setose (80.0%), rarely setiferous (20.0%); mandibles simple, with two apical teeth per mandible, usually setose (80.0%), rarely setiferous (20.0%); antennae with 27–29 flagellomeres. *Mesosoma*: 0.38–0.46 mm wide; 0.64–0.75 mm long; 0.59–0.63× as wide as long; 0.71–0.74× as wide as deep; 1.14–1.21× as long as deep; pronotum coriaceous laterally, crenulate in anterior furrow; notauli represented by anterior depressions; mesoscutum smooth, setiferous anteriorly and along lines where notauli would run if present; mesopleuron nearly entirely smooth, rugulose to crenulate near tegulae, sternaulus distinctly crenulate; scutellar disc smooth; propodeum rugose, setiferous; metapleuron usually setiferous (80.0%), rarely setose (20.0%). *Metasoma*: t1 0.70–1.20× as wide as long, longitudinally rugulose with two prominent dorsal carinae converging posteriorly; t2 coriaceous; t3 coriaceous; remaining tergites smooth; exposed ovipositor 0.18–0.32 mm long. *Legs*: smooth, setiferous, hind tibia 0.96–1.02× as long as mesosoma length. *Wings*: hyaline; forewing stigma narrow and elongate; 2RS 0.52–0.62× as long as 3RSa; 2RS 0.41–0.47× as long as 2M; 3RSa 0.75–0.82× as long as 2M. *Color*: head mostly yellow, vertex very dark brown to black; mesosoma very dark brown to black, mesopleuron occasionally yellowish orange ventrally and near tegulae; t1 brown to dark brown medially, yellow laterally; t2 yellow; t3 yellow with posterior edge dark

brown; t4 dark brown medially, yellow laterally, and posterior edge dark brown (60.0%) or t4 mostly yellow with posterior edge dark brown (40.0%); remaining tergites dark brown medially, yellow laterally, and posterior edge dark brown; legs orangish yellow to yellow, posterior portion of metatibia and entire metatarsus yellowish brown.

**Male.**—As in ♀ except: *Head*: 1.19–1.27× as wide as long; eyes 0.63–0.71× as wide as long; antennae with 26–27 flagellomeres. *Mesosoma*: 0.35–0.42 mm wide; 0.59–0.70 mm long; 0.57–0.65× as wide as long; 0.67–0.77× as wide as deep; 1.12–1.30× as long as deep; mesoscutum usually smooth (80.0%), occasionally minutely coriaceous (20.0%). *Legs*: hind tibia 0.90–1.03× as long as mesosoma length. *Wings*: 2RS 0.42–0.48× as long as 2M. *Color*: mesosoma usually very dark brown to black (80.0%), rarely dark reddish brown (20.0%); t1 entirely dark brown (40.0%) or t1 dark brown medially and yellow laterally (40.0%) or t1 reddish brown medially and yellow laterally (20.0%); t4 usually dark brown (80.0%), rarely brown medially, yellow laterally, and posterior edge dark brown (20.0%); remaining tergites dark brown.

**Host.**—Unknown.

**Material examined.**—Holotype ♀: USA, South Carolina, Greenville County, Greenville, 18.ix.1955, G. and L. Townes (AEI). Allotype ♂: same data as holotype except 6.vii.1952 (AEI). Other determined material: all USA, North Carolina, Transylvania County, Pisgah National Forest except 1♀, South Carolina, Greenville County, Paris Mountain State Park, 16.–21.v.1999, R. R. Kula, Malaise trap; 1♀, Coontree Creek Trail, 17.–21.v.1999, R. R. Kula, Malaise trap; 1♀, Pink Beds, 17.v.1999, R. R. Kula, sweep net; 1♀, 3♂, Coontree Creek Trail, 18.v.1999, R. R. Kula, sweep net; 1♂, Pink Beds, 19.v.1999, R. R. Kula, sweep net (det. Kula) (TAMU).

**Diagnosis.**—Within the *striativentris*-group *O. clevelandensis* Fischer, *O. niobe*,

and *O. weemsi* are morphologically similar to *O. intermissus*. Head coloration can be used to distinguish *intermissus* from all three species. The head is yellow with a very dark brown to black vertex in *intermissus*. The head is yellowish brown with a brown vertex in *clevelandensis*, entirely brown to yellowish brown in *niobe*, and mostly orange with a very dark brown vertex and a partially brown face in *weemsi*. Mesosomal coloration can also be used to distinguish *intermissus* from *clevelandensis* and *niobe*. In *intermissus* the mesosoma is usually very dark brown to black, while in *clevelandensis* and *niobe* the mesosoma is brown to dark brown. Additionally, *intermissus* can be distinguished from *clevelandensis* and *weemsi* using exposed ovipositor length and the number of antennal flagellomeres, respectively. In *intermissus* the ovipositor is relatively short (exposed ovipositor 0.18–0.32 mm long) and barely exserted from the abdomen, while in *clevelandensis* the ovipositor is long (exposed ovipositor 1.12 mm long) and conspicuously exserted from the abdomen. The number of flagellomeres in *intermissus* is 26–29, as opposed to 32 in *weemsi*.

**Discussion.**—*Opius intermissus* falls within the *striativentris*-group. Dark brown mesosomal coloration was observed in only one male specimen, and all other specimens have a very dark brown to black mesosoma. Distinct color differences were observed between female and male specimens. In females t4 is dark brown medially and yellow laterally or mostly yellow with the posterior edge dark brown. In males t4 is usually entirely dark brown to black. Yellow coloration on t4 was observed in only one male specimen. No biological data are associated with *intermissus*, but other species in the *striativentris*-group have been reared from leaf mining Agromyzidae (e.g. *O. abyiae*, *O. adductus*, *O. striativentris*).

#### *Opius (Gastrosema) oscinidis (Ashmead)*

*Rhyssalus oscinidis* Ashmead 1889 (1888): 630.  
*Eutrichopsis oscinidis*: Viereck 1913: 559.

*Opius oscinidis*: Gahan 1915: 72, 90.

*Opius (Aulonotus) oscinidis*: Fischer 1977: 78, 87.

*Opius pusilloides* Fischer 1964: 413, 433. Synonym

Marsh (1974).

**Female.**—**Head:** 1.21–1.35× as wide as long; eyes 0.65–0.72× as wide as long, glabrous; face entirely smooth to entirely rugulose, slightly raised mesally, usually setose (81.8%), rarely setiferous (18.2%); clypeus flattened to convex, ventral margin lobed mesally, usually setose (81.8%), rarely setiferous (18.2%); mandibles simple, with two apical teeth per mandible, setiferous; antennae with 21–22 flagellomeres. **Mesosoma:** 0.38–0.43 mm wide; 0.66–0.75 mm long; 0.53–0.60× as wide as long; 0.73–0.79× as wide as deep; 1.34–1.42× as long as deep; pronotum smooth laterally, crenulate in anterior furrow; notauli represented by anterior depressions; mesoscutum smooth, setiferous anteriorly and along lines where notauli would run if present; mesopleuron nearly entirely smooth, slightly to distinctly crenulate near tegulae, sternaulus distinctly crenulate; scutellar disc smooth; propodeum rugose, especially medially, setose; metapleuron setose. **Metasoma:** t1 0.69–1.00× as wide as long, longitudinally rugulose with two prominent dorsal carinae delimiting a raised median area; t2 often longitudinally carinate at posterior edge (63.6%), occasionally longitudinally carinate medially (36.4%); t3 often smooth (63.6%), occasionally longitudinally carinate at anterior edge (36.4%); remaining tergites smooth; exposed ovipositor 0.16–0.46 mm long. **Legs:** smooth, setiferous, hind tibia 0.91–1.00× as long as mesosoma length. **Wings:** hyaline; forewing stigma narrow and elongate; 2RS 0.42–0.59× as long as 3RSa; 2RS 0.33–0.43× as long as 2M; 3RSa 0.73–0.80× as long as 2M. **Color:** face and clypeus brownish yellow, remainder of head brown (54.6%) or head entirely brown (27.3%) or face and clypeus yellow, remainder of head brown (18.2%); mesosoma brown to dark brown; t1 dark brown;

t2 yellow (54.6%) or yellowish brown (45.5%); t3 often yellowish brown (63.6%), occasionally anterior half yellow, posterior half brown (27.3%), rarely anterior two thirds yellow, posterior one third brown (9.1%); t4 usually brown to dark brown (90.9%), rarely yellowish brown (9.1%); remaining tergites brown to dark brown; legs orangish yellow to yellow.

**Male.**—As in ♀ except: *Head*: 1.19× as wide as long. *Mesosoma*: 0.37 mm wide.

**Hosts.**—An undetermined species of *Chlorops* Meigen on *Plantago major* L. (Ashmead 1889); *Phytomyza orobanchia* Kaltenbach (Hennig 1953); *Ph. plantaginis* Robineau-Desvoidy (Muesebeck and Walkley 1951). All records need verification.

**Material examined.**—Holotype ♀, *O. oscinidis*: no locality data (USNM). Holotype ♀, *O. pusilloides*: USA, Allegany County, Thomas Road near Cumberland, 28.vi.1953, L. M. Walkley (USNM). Allotype ♂, *O. pusilloides*: USA, Maryland, Montgomery County, Cabin John, 21.viii.1917, R. M. Fouts (USNM). Paratypes *O. pusilloides*: all USA; 1♀, New York, Otsego County, Oneonta, 24.viii.1935, H. K. Townes; 1♀, New York, Otsego County, Oneonta, 2.ix.1935, H. K. Townes; 1♀, New York, Tompkins County, Ithaca, 7.ix.1935, H. K. Townes; 1♀, New York, Tompkins County, Ithaca, 11.ix.1935, H. K. Townes; 1♀, North Carolina, Transylvania County, Pink Beds, 22.vii.1952, G. and L. Townes; 1♀, North Carolina, Henderson County, Flat Rock, 6.ix.1952, G. and L. Townes; 1♀, South Carolina, Greenville County, Greenville, 24.v.1952, G. and L. Townes; 1♀, South Carolina, Greenville County, Greenville, 1.ix.1952, L. and G. Townes; 1♀, South Carolina, Greenville County, Greenville, 7.ix.1952, L. and G. Townes (AEI). Other determined material: 1♀, South Carolina, Greenville County, Greenville, 1.x.1954, G. and L. Townes (det. Fischer as *pusilloides*) (AEI).

**Diagnosis.**—*Opicus oscinidis* is extremely different morphologically from all described Nearctic species in *Gastrosema*. In

*oscinidis* t2 is at least partially longitudinally carinate, although it is nearly smooth in some individuals. Thus, *oscinidis* can be differentiated from all species in the *striativentris*-group based on tergite sculpture. *Opicus oscinidis* lacks crenulations above the episternal scrobe in the posterior mesopleural furrow. Thus, *oscinidis* can be differentiated from all species in the *flaviceps*-group based on posterior mesopleural furrow sculpture. Additionally, *oscinidis* has a narrowly elongate second submarginal cell, while species in the *striativentris*-group often have a narrow but relatively short second submarginal cell. The second submarginal cell is shape variable for species in the *flaviceps*-group, but a narrowly elongate second submarginal cell, as exemplified by *oscinidis*, has not been observed for species in the *flaviceps*-group.

**Discussion.**—*Opicus oscinidis* falls within the *oscinidis*-group. Marsh (1974) synonymized *O. pusilloides* with *oscinidis*. Comparison of the holotypes for *oscinidis* and *pusilloides* with a long series of determined *pusilloides* from the AEI and USNM verified the synonymy. Of the 21 described Nearctic species in *Gastrosema*, *O. oscinidis* is the only species that falls within the *oscinidis*-group. However, several species in other subgenera fit within the *oscinidis*-group (as noted above). All biological data associated with *oscinidis* needs verification. *Opicus oscinidis* is morphologically similar to a species of *Opicus* near *extiratus* that has been reared from *Phytomyza* spp. mining the leaves of hollies.

### *Opicus (Gastrosema) salmonensis* Fischer

*Opicus salmonensis* Fischer 1964: 412, 438.

*Opicus (Gastrosema) salmonensis*: Fischer 1977: 313, 385.

**Female.**—*Head*: 1.36–1.47× as wide as long; eyes 0.77–0.88× as wide as long, glabrous; face punctate, slightly raised mesally, setose; clypeus broadly hemielliptical, usually flattened (80.0%), rarely weak-

ly convex (20.0%), ventral margin straight to slightly arched, often setose (60.0%), occasionally setiferous (40.0%); mandibles simple, with two apical teeth per mandible, often setose (60.0%), occasionally setiferous (40.0%); antennae with 21–28 flagellomeres. *Mesosoma*: 0.61–0.86 mm wide; 1.02–1.36 mm long; 0.57–0.64× as wide as long; 0.71–0.79× as wide as deep; 1.25–1.31× as long as deep; pronotum smooth to rugose laterally, rugose to crenulate in anterior and posterior furrows; notaui represented by deep anterior depressions; mesoscutum often smooth (60.0%), occasionally minutely coriaceous (40.0%), usually setose anteriorly and along lines where notaui would run if present (80.0%), rarely entirely setose (20.0%); mesopleuron minutely coriaceous, deeply crenulate near tegulae, sternaulus broadly crenulate to broadly lacunose; scutellar disc often smooth (60.0%), occasionally minutely coriaceous (40.0%); propodeum areolate-rugose, setiferous; metapleuron often setose (60.0%), occasionally setiferous (40.0%). *Metasoma*: t1 0.84–1.11× as wide as long, usually costate (80.0%), rarely rugose (20.0%); t2 costate; t3 often longitudinally carinate in anterior half and smooth in posterior half (60.0%), rarely entirely minutely coriaceous (20.0%) or entirely smooth (20.0%); remaining tergites smooth; exposed ovipositor 0.64–1.52 mm long. *Legs*: smooth, setiferous, hind tibia 0.73–0.84× as long as mesosoma length. *Wings*: hyaline; forewing stigma broad and wedge shaped; 2RS 0.57–0.67× as long as 3RSa; 2RS 0.42–0.45× as long as 2M; 3RSa 0.67–0.75× as long as 2M. *Color*: head mostly yellow (80.0%) or orangish yellow (20.0%), vertex dark brown, at least around ocelli; mesosoma usually very dark brown (80.0%), rarely reddish brown (20.0%); t1 usually dark brown (80.0%), rarely reddish brown (20.0%); t2 usually yellow (40.0%) or orangish yellow (40.0%), rarely reddish brown (20.0%); t3 anterior half yellow, posterior half dark brown (20.0%) or t3 anterior half orangish yellow,

posterior half dark brown (20.0%) or t3 anterior one third orangish yellow, posterior two thirds dark brown (20.0%) or t3 entirely reddish brown (20.0%) or t3 entirely dark brown (20.0%); remaining tergites dark brown; legs yellow, metatibia and metatarsus usually yellow (80.0%), rarely yellowish brown (20.0%).

*Male*.—As in ♀ except: *Head*: face punctate (50.0%) or rugulose (50.0%); clypeus flattened, setiferous (50.0%) or setose (50.0%); mandibles setose; antennae with 23–30 flagellomeres. *Mesosoma*: 0.56–0.67 mm wide; 0.55–0.59× as wide as long; 0.70–0.77× as wide as deep; pronotum often minutely coriaceous laterally (75.0%), occasionally smooth laterally (25.0%); mesoscutum often minutely coriaceous (75.0%), occasionally smooth (25.0%), setose anteriorly and along lines where notaui would run if present; scutellar disc often minutely coriaceous (75.0%), occasionally smooth (25.0%); metapleuron often setose (75.0%), occasionally setiferous (25.0%). *Metasoma*: t1 0.79–1.00× as wide as long, rugose (50.0%), longitudinally rugose (25.0%), or costate (25.0%); t2 costate (50.0%), coriaceous (25.0%), or smooth with anterior edge longitudinally carinate (25.0%); t3 smooth (50.0%), minutely coriaceous (25.0%), or minutely coriaceous with anterior edge longitudinally carinate (25.0%); remaining tergites smooth. *Wings*: 2RS 0.61–0.75× as long as 3RSa; 2RS 0.43–0.50× as long as 2M; 3RSa 0.63–0.70× as long as 2M. *Color*: head mostly yellow, vertex dark brown; mesosoma very dark brown; t1 dark brown; t2 yellow (50.0%), orangish yellow (25.0%), or brownish yellow (25.0%); t3 anterior one third brownish yellow, posterior two thirds dark brown (25.0%) or t3 anterior half orangish yellow, posterior half dark brown (25.0%) or t3 anterior half yellow, posterior half dark brown (25.0%) or t3 anterior two thirds yellow, posterior one third dark brown (25.0%); remaining tergites dark brown; legs yellow, metatarsus often yel-

low (75.0%), occasionally yellowish brown (25.0%).

*Host.*—Unknown.

*Material examined.*—Holotype ♀: CANADA, British Columbia, Salmon Arm, shore of Shuswap Lake, 13.vii.1949, H. B. Leech (CAS). Other determined material: 2♂, CANADA, Province Québec, 50°03'N 77°07'W, 12.vi.–8.viii.1987, Leblanc (AEI); 1♀ USA, New Hampshire, Grafton County, Mount Cardigan (USNM); 1♀, USA, North Carolina, Macon County, Highlands, 22.vi.1977, H. and M. Townes; 1♀, USA, North Carolina, Macon County, Highlands, 26.vi.1977, H. and M. Townes; 1♀, USA, Wisconsin, Grant County, T6N R6W S17, 29.v.–3.vi.1975, gypsy moth Malaise trap; 1♂, USA, Wisconsin, Fond du Lac County, T13N R19E S23, 11.–18.vi.1975, gypsy moth Malaise trap; 1♂, USA, Wisconsin, Jackson County, T21N R4W S27, 16.–23.vi.1975, gypsy moth Malaise trap (det. Kula) (AEI).

*Diagnosis.*—Within the *flaviceps*-group *O. flaviceps* is morphologically similar to *O. salmonensis*. *Opicus salmonensis* is conspicuously smaller than *flaviceps*. In *salmonensis* the mesosoma is 1.02–1.36 mm long, while in *flaviceps* the mesosoma is 1.84 mm long. In *salmonensis* the mesosoma is 0.56–0.86 mm wide, while in *flaviceps* the mesosoma is 0.98 mm wide. Additionally, exposed ovipositor length in *salmonensis* is 0.64–1.52 mm, as opposed to 1.78 mm in *flaviceps*.

*Discussion.*—*Opicus salmonensis* falls within the *flaviceps*-group. One specimen of *salmonensis* in the USNM and five specimens of *salmonensis* in the AEI were misidentified as *O. flaviceps*. All specimens differ from the holotype of *flaviceps* in size and exposed ovipositor length (as detailed in the diagnosis for *salmonensis*).

Size differences were observed between female and male specimens of *salmonensis*. In females the mesosoma is 0.61–0.86 mm wide, while in males the mesosoma is 0.56–0.67 mm wide. In females the maximum mesosoma length is 1.36 mm, and in

males the maximum mesosoma length is 1.15 mm. Differences in sculpture on t2 were also observed between the sexes. In females t2 is always costate, while in males t2 may be costate, coriaceous, or smooth with the anterior edge longitudinally carinate. Sculpture on t2 is generally reduced in males relative to females.

Unfortunately, no biological data are associated with *salmonensis*. However, the ovipositor of *salmonensis* is long relative to species that have been reared from leaf mining Agromyzidae (e.g. *O. abyae*, *O. adductus*, *O. striativentris*). This suggests that *salmonensis* may attack a non-leaf miner host in a concealed situation.

#### *Opicus (Gastrosema) striativentris* Gahan

*Opicus striativentris* Gahan 1915: 72, 89.

*Opicus (Gastrosema) striativentris*: Fischer 1977: 312, 393.

*Opicus gracillariae* Gahan 1915: 72, 90. **New synonym.**

*Female.*—*Head*: 1.24–1.48× as wide as long; eyes 0.63–0.79× as wide as long, glabrous; face usually smooth with rugulose sculpture between antennal sockets and compound eyes (86.4%), rarely entirely smooth (13.6%), slightly raised (60.9%) or flattened (39.1%) mesally, setiferous; clypeus hemispherical to narrowly hemielliptical, convex, ventral margin straight to slightly arched, setiferous; mandibles simple, with two apical teeth per mandible, setiferous; antennae with 18–22 flagellomeres. *Mesosoma*: 0.35–0.50 mm wide; 0.56–0.82 mm long; 0.56–0.65× as wide as long; 0.78–1.00× as wide as deep; 1.31–1.61× as long as deep; pronotum usually coriaceous laterally (92.1%), rarely entirely smooth (4.6%) or dorsal half smooth ventral half coriaceous (3.4%), usually crenulate in anterior furrow (96.6%), rarely smooth (3.4%); notauli represented by anterior depressions; mesoscutum usually smooth (94.3%), rarely rugulose medially near transscutal articulation (5.7%), usually setiferous anteriorly and along lines where notauli would run if present

(86.4%), rarely setiferous anteriorly only (9.1%) or glabrous (4.6%); mesopleuron nearly entirely smooth, often smooth near tegulae (55.5%), occasionally rugulose to crenulate near tegulae (44.5%), sternaulus usually crenulate (86.4%), rarely rugulose (10.2%) or reduced to a smooth depression (3.41%); scutellar disc smooth; propodeum rugulose to rugose, usually setiferous (98.9%), rarely glabrous (1.1%); metapleuron usually setiferous (98.9%), rarely glabrous (1.1%). *Metasoma*: t1 1.00–1.56× as wide as long, usually rugulose (87.4%), rarely rugose (11.5%) or smooth (1.2%); t2 coriaceous; t3 coriaceous; t4 often smooth (59.8%), occasionally coriaceous (33.3%); remaining tergites smooth; ovipositor 0.37–0.48 mm long. *Legs*: smooth, setiferous, hind tibia 0.82–0.95× as long as mesosoma length. *Wings*: hyaline; forewing stigma narrow and elongate; 2RS 0.50–0.69× as long as 3RSa; 2RS 0.40–0.52× as long as 2M; 3RSa 0.73–0.87× as long as 2M. *Color*: head entirely dark brown to orangish yellow with vertex dark brown to black; mesonotum often brown to dark brown and conspicuously darker than rest of mesosoma (63.6%), occasionally entirely brownish orange to dark brown (36.4%); t1 usually yellow to brownish orange (94.3%), rarely light orangish brown (4.6%) or yellowish brown (1.2%); t2 brownish orange to yellow; t3 brownish orange to yellow; remaining tergites dark brown to orangish yellow; legs yellow, metatibia and metatarsus yellow to yellowish brown.

*Male*.—As in ♀ except: *Head*: 1.23–1.39× as wide as long; eyes 0.67–0.80× as wide as long; face often with rugulose sculpture between antennal sockets and compound eyes (73.3%), occasionally entirely smooth (26.7%). *Mesosoma*: 0.34–0.43 mm wide; 0.55–0.65× as wide as long; 0.77–0.90× as wide as deep; pronotum usually coriaceous laterally (86.7%), rarely smooth (13.3%), usually crenulate in anterior furrow (86.7%), rarely smooth (13.3%); mesoscutum usually smooth (96.7%), rarely

rugulose medially near transscutual articulation (3.33%), usually setiferous anteriorly and along lines where notauli would run if present (93.3%), rarely setiferous anteriorly only (6.7%); mesopleuron nearly entirely smooth, often crenulate near tegulae (70.0%), occasionally smooth near tegulae (30.0%), sternaulus usually crenulate (86.7%), rarely reduced to a smooth depression (13.3%). *Wings*: 2RS 0.55–0.71× as long as 3RSa.

*Hosts*.—*Phytomyza glabricola* Kulp mining the leaves of *Ilex coriacea* (Pursh) and *I. glabra* (L.); *P. ilicicola* Loew (as *P. ilicis* Curtis) mining the leaves of *I. opaca* Soland. in Ait. (Langford and Cory 1937); *P. vomitoriae* Kulp mining the leaves of *I. vomitoria* Soland. in Ait.

*Material examined*.—Holotype ♀, *O. striativentris*: no locality data (USNM). Holotype ♀, *O. gracillariae*: no locality data (USNM). Other determined material: all USA; 1♀, Louisiana, Cameron Parish, Route 27, 2.i.1998, S. Scheffer; 1♀, Mississippi, Forrest County, De Soto National Forest, Route 13, 7.i.1998, S. Scheffer; 3♀, North Carolina, Montgomery County, Uwharrie National Forest, i.1996, S. Scheffer; 14♀, North Carolina, Moore County, Ebersole Holly Garden, 21.ii.1996, S. Scheffer; 6♀, North Carolina, Wake County, North Carolina State University Arboretum, 23.ii.1996, S. Scheffer; 1♀, North Carolina, New Hanover County, Carolina Beach State Park, 24.ii.1996, S. Scheffer; 1♀, North Carolina, iv.1996; 8♀, North Carolina, New Hanover County, Carolina Beach State Park, marina, 21.ii.1997, S. Scheffer; 3♀, North Carolina, New Hanover County, Carolina Beach State Park, Flytrap Trail, 26.i.1998, S. Scheffer; 26♀, 30♂, South Carolina, Berkeley County, Francis Marion National Forest, Big Ocean Bay, 18.ii.1997, S. Scheffer; 8♀, South Carolina, Charleston County, Francis Marion National Forest, Buck Hall, 19.ii.1997, S. Scheffer; 5♀, South Carolina, Berkeley County, Francis Marion National Forest, North Honey Hill Road, 19.ii.1997, S.

Scheffer; 1♀, South Carolina, Berkeley County, Francis Marion National Forest, Road 188, 19.ii.1997, S. Scheffer; 7♀, South Carolina, Berkeley County, Francis Marion National Forest, Big Ocean Bay, 21.i.1998, S. Scheffer; 2♀, Tennessee, Shelby County, Memphis Botanical Garden, 29.viii.1997, S. Scheffer; 1♀, Texas, Jasper County, Angelina National Forest, Boykin Springs Trail, 2.i.1998, S. Scheffer (det. Kula as *striativentris*) (TAMU).

**Diagnosis.**—Within the *striativentris*-group *O. castaneigaster* and *O. hancockanus* are morphologically similar to *O. striativentris*. Characters used to differentiate *striativentris* from *castaneigaster* can be found in the diagnosis for *castaneigaster*. The shape of the mesosoma and t1 width to length ratios can be used to distinguish *striativentris* from *hancockanus*. In *striativentris* the mesosoma is 1.31–1.61× as long as deep and similar in shape to *castaneigaster*. In *hancockanus* the mesosoma is 1.26× as long as deep and similar in shape to *niobe*. Tergite 1 is 1.00–1.56× as wide as long in *striativentris*, while t1 is 0.65× as wide as long in *hancockanus*.

**Discussion.**—*Opius striativentris* falls within the *striativentris*-group. In Fischer's subgeneric classification individuals with a crenulate sternaulus fall within *Gastrosema*, but individuals with a smooth sternaulus fall within *Merotrachys*. *Opius striativentris* is retained in *Gastrosema* because the majority of individuals (i.e. 91.7%) fall within *Gastrosema*.

Comparison of the holotype of *O. gracillariae* with hundreds of *striativentris* specimens revealed that *gracillariae* falls within the morphological limits of *striativentris* as defined in this study. Thus, *O. gracillariae* Gahan 1915 is a new synonym of *O. striativentris* Gahan 1915. The holotype of *gracillariae* is morphologically similar to *striativentris* reared from *P. glabricola* infesting *I. coriacea* and *I. glabra*. *Opius gracillariae* and *striativentris* were both originally described in Gahan (1915). *Opius striativentris* is designated the senior

synonym because the name *striativentris* has been associated with a greater number of studies and appears more frequently in the literature than *gracillariae*. Gahan (1915) reported that *gracillariae* was reared from *Porphyrosela desmiodella* (Clément). This record is clearly invalid because *P. desmiodella* is a lepidopteran. Opiinae, as currently defined, is limited to braconids that are endoparasitoids of cyclorrhaphous Diptera. However, *Porphyrosela desmiodella* feeds on *Desmodium* Desv., and *Japanagromyza desmodivora* Spencer is an agromyzid that mines the leaves of *D. tortuosum* DC. Thus, Gahan's *gracillariae* may have actually been reared from an agromyzid.

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## *Prosopigastra morogoro*, a New Species from Tanzania (Hymenoptera: Apoidea: Crabronidae: Larrini)

WOJCIECH J. PULAWSKI

Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA; email: wpuławski@calacademy.org

**Abstract.**—The new species *Prosopigastra morogoro* Pulawski, from Tanzania, is characterized by a densely punctate frontal protuberance and gena, an unusual female pygidial plate, presence of a male pygidial plate, and unique male sternum VII. Its closest congener is the southern African *capensis* Brauns. Several corrections are made to an earlier diagnosis of the genus by Pulawski, 1979.

I revised the world species of *Prosopigastra* more than twenty years ago (Pulawski 1979). During a collecting trip to Tanzania in 2001, I discovered a spectacular undescribed species apparently never collected before. Its discovery requires three corrections to my earlier diagnosis of the genus: 1) The marginal cell is longer than in other members of the genus and is not broadly truncate, its length being  $2.6\text{--}2.9 \times$  maximum width of the cell (inner dimensions) rather than 1.6–2.3, and the distance between its posteroapical corner equaling 1.1–1.4× its maximum width. Contrary to my original statement, the cell length of the new species overlaps with those of *Holotachysphex*, *Parapiagetia*, and *Tachysphex* and therefore is not diagnostic for the entire genus. 2) The pygidial plate of the female has a number of large, ill-defined punctures on its entire surface. The presence of an adlateral row of punctures, therefore, is not diagnostic for the entire genus. 3) Similarly, male tergum VII has a well-defined pygidial plate and lacks a translucent, impunctate apical depression. The presence of the depression and lack of a pygidial plate are not characteristics of the entire genus.

The terminology in the following description is as in Pulawski (1979).

### *Prosopigastra morogoro* Pulawski, new species

**Name derivation.**—Morogoro, a town in Tanzania in whose vicinity the species was first discovered; a noun in apposition.

**Recognition.**—*Prosopigastra morogoro* is unique in having a conspicuous, densely punctate frontal protuberance and a uniformly, densely punctate gena, with punctures one diameter apart or less. In other *Prosopigastra*, the frontal protuberance is either prominent and impunctate or punctate and inconspicuous, and the genal punctures are several to many diameter apart, at least near the hypostomal carina. Also, the marginal cell of *morogoro* is longer than in any other species, its anterior margin being  $2.6\text{--}2.9 \times$  maximum cell width (inner dimensions) rather than 1.6–2.3. The female has irregular, large punctures on the entire pygidial plate (Fig. 1d). In the male, tergum VII has a well-defined pygidial plate (unlike any other *Prosopigastra*), and sternum VIII is thickened near the apex, the thickening having an apical concavity (Fig. 2d, f), possibly a unique feature among Apoidea.

**Description.**—Frons microridged between antennal socket and protuberance; protuberance prominent, punctate throughout (punctures less than one diameter apart). Middle clypeal section convex, with minute carina emerging from corner of clypeal lobe and nearly parallel to clypeal free margin; lip slightly, obtusely pointed mesally, not incised laterally. Gena densely, uniformly punctate throughout, punc-

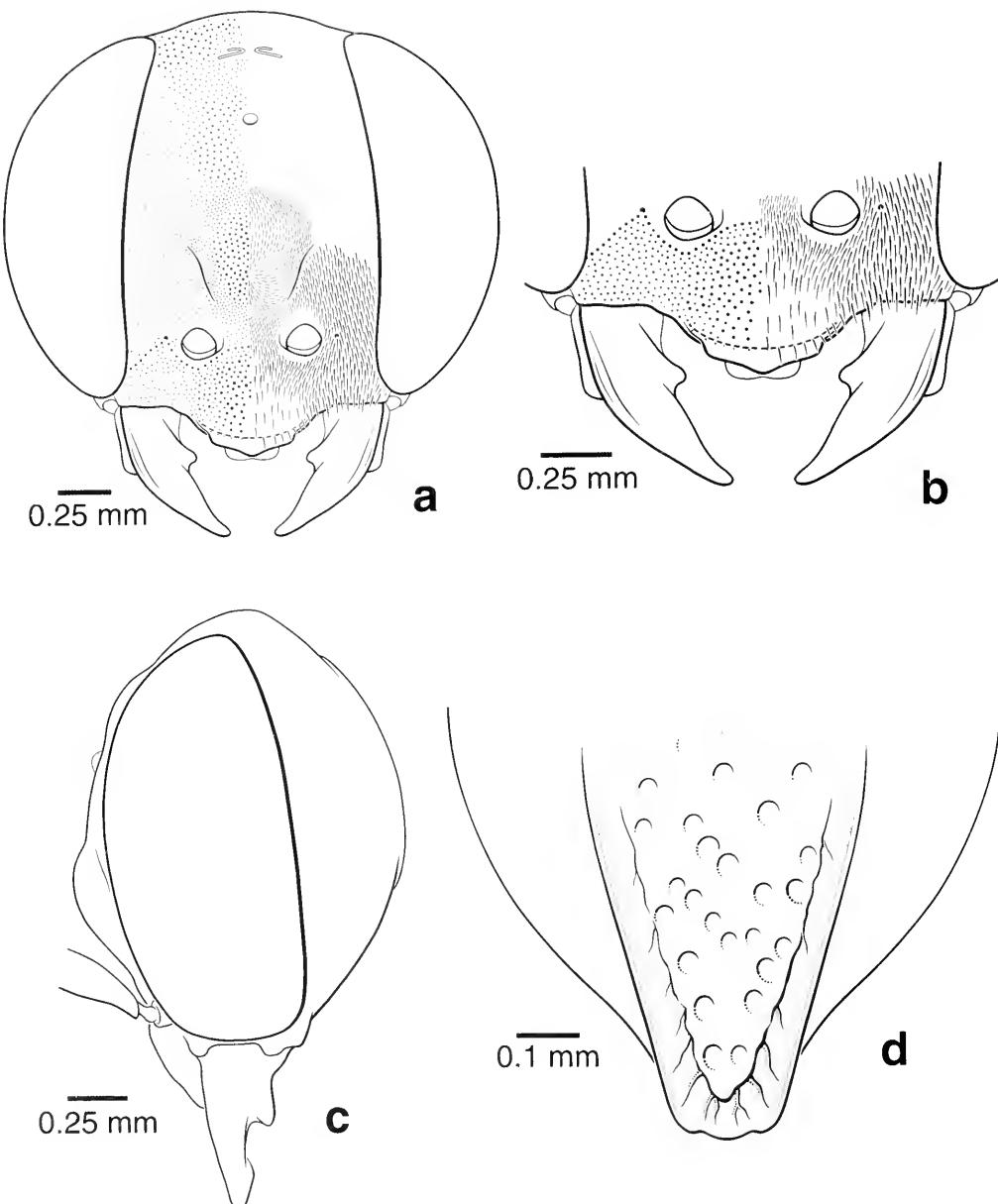


Fig. 1. *Prospigastra morogoro*, female: a—head in frontal view, b—clypeus, c—head in lateral view, d—pygidial plate.

tures no more than one diameter apart. Ventral mandibular margin step-like, without preapical expansion at distal end of notch (hence notch open distally). Mesopleuron either punctate (punctures less than one diameter apart) or punctatorugose, with small unsculptured area above scrobe. Precoxal mesopleural carina

sharp, expanded into spine in male. Propodeal dorsum with longitudinal, anastomosed ridges, in some specimens irregularly rugose mesally. Marginal cell with dense microtrichia, its anterior margin longer than pterostigma, with length  $2.6-2.9 \times$  maximum cell's width (inner dimensions), apical truncation oblique; distance

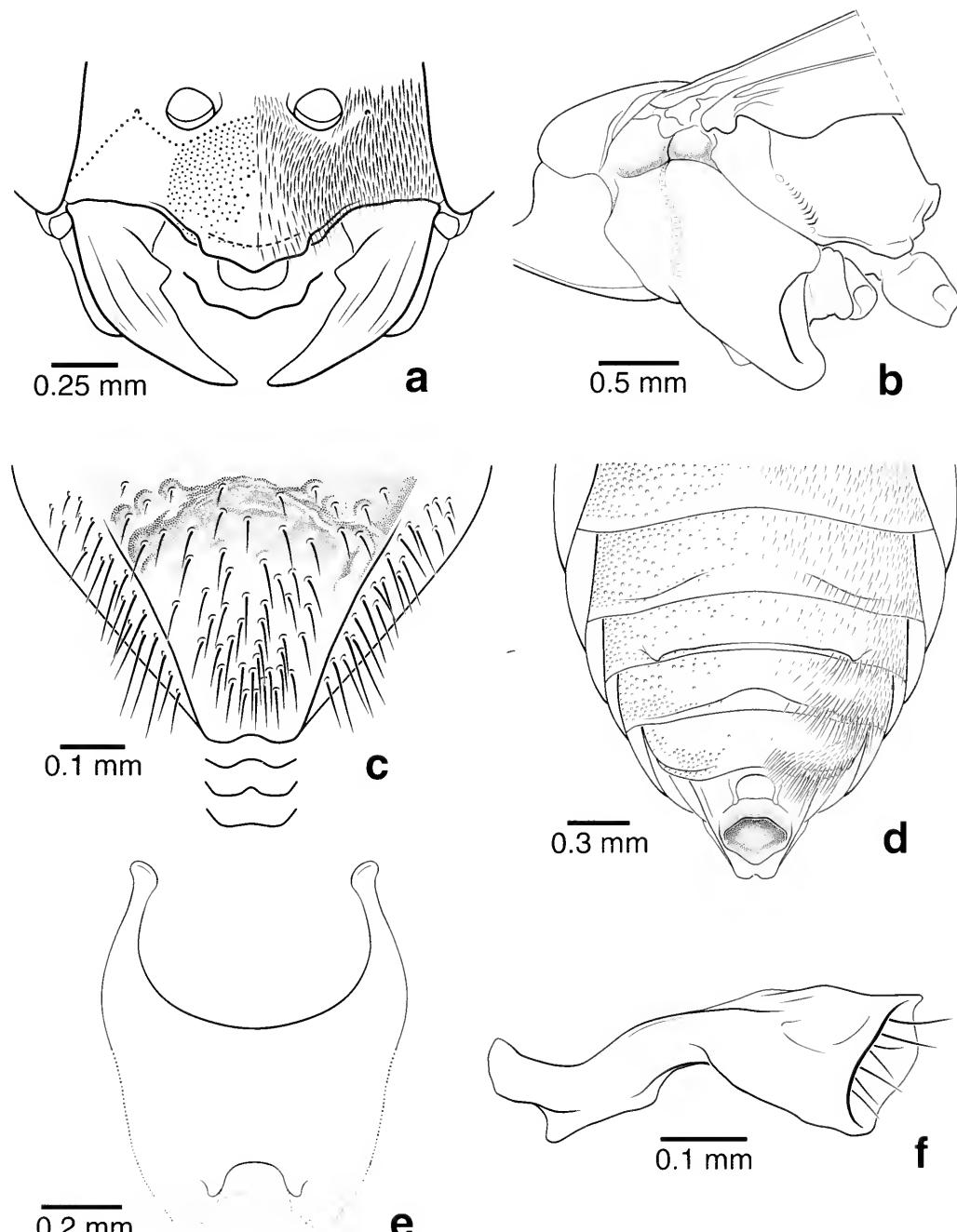


Fig. 2. *Prospigastra morogoro*, male: a—clypeus, b—thorax in lateral view, c—pygidial plate, d—gastral sternum, e—sternum VII, f—sternum VIII in oblique lateral view.

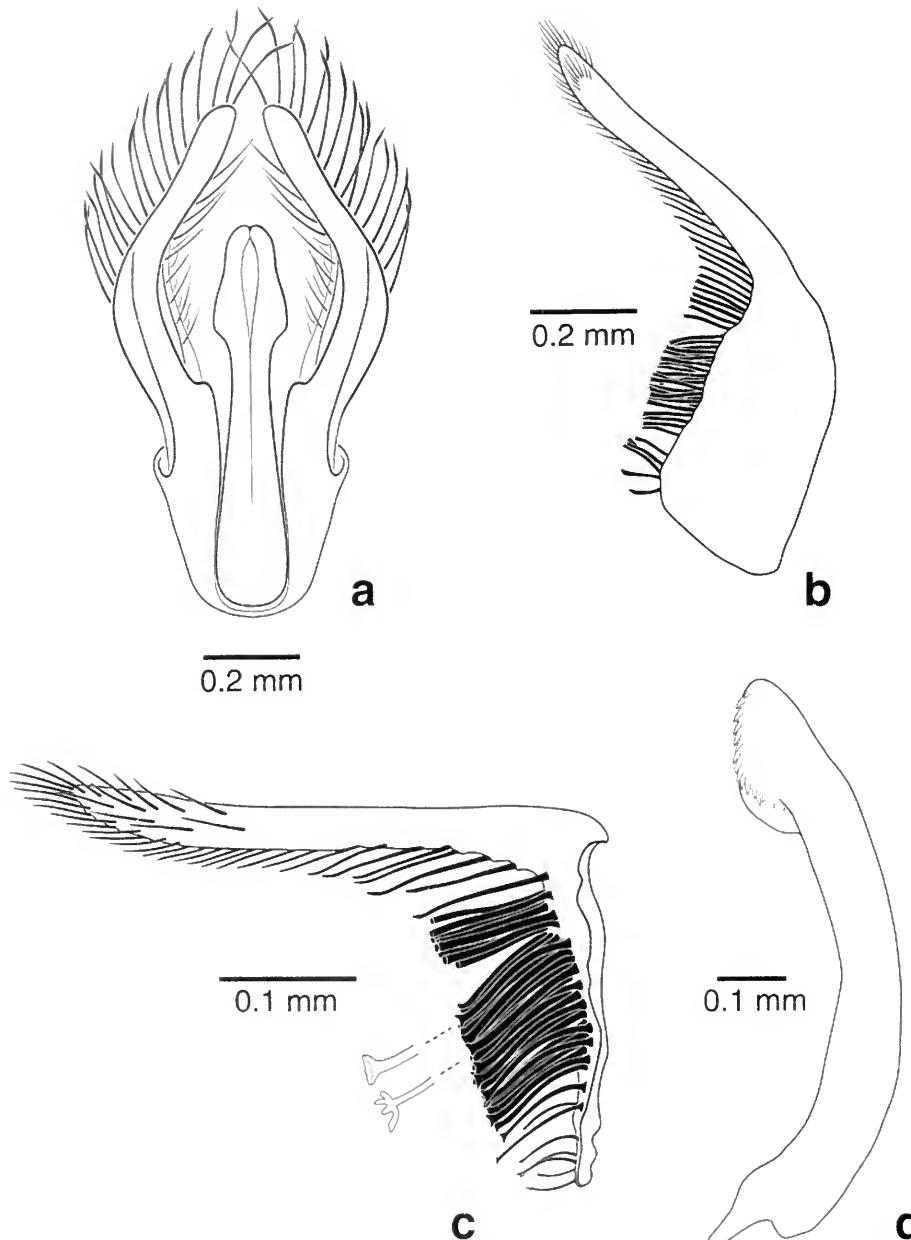


Fig. 3. *Prosopigastra morogoro*, male genitalia: a—dorsal view, b—gonoforceps in lateral view, c—volsella, d—penis valve.

between cell's posteroapical corner and anterior margin equal to 1.1–1.4× cell's maximum width. Punctures less than one diameter apart between midocellus and orbit and on gena (except dorsally), no more than one diameter apart on intercellular area and scutum; less than one

diameter apart on hindfemoral outer surface except more than one diameter apart along ventral margin in female. Gastral terga coarsely punctate, terga I and II each with lateral line (lateral carina of Pulawski, 1979). Setae inclined anterad on vertex, about 1.5× as long as mi-

postocellar diameter, on scutum inclined posterad, shorter than midocellar diameter (longest near anterior margin). Mesopleural vestiture not obscuring integument. Upper metapleuron largely glabrous. Tergum I without tomentum in female, with rudimentary tomentum just posterad of basal declivity in many males. Body black except mandible reddish preapically in female and yellowish white in basal two thirds in male and tarsal apex brown. Wing membrane slightly infumate, veins dark brown.

**Female.**—Clypeus (Fig. 1a): lip slightly, obtusely pointed mesally, not incised laterally. Width of postocellar area about  $2.5 \times$  length. Precoxal mesopleural carina sharp. Pygidial plate with irregular, large punctures, without setae in unique specimen in unique specimen, probably due to abrasion (Fig. 1d). Length 7.5 mm.

**Male.**—Flagellum cylindrical. Width of postocellar area  $1.7\text{--}2.1 \times$  length. Mesothoracic venter deeply concave; precoxal mesopleural carina expanded into prominent spine (which is disproportionately larger in large specimens); spine connected by carina to apophysis-like signum. Tergum VII with well defined pygidial plate (Fig. 2c). Sterna III–VI shallowly concave mesally; sterna V and VI posterolaterally each with conspicuous tuft of setae; sternum VII with apical emargination that is partly covered by membrane (Fig. 2e); sternum VIII conspicuously thickened apically, with apical surface of thickening characteristically concave (2f). Length 6.1–8.5 mm. Genitalia, gonoforceps, volvella, and penis valve: Fig. 3a–d.

**Relationships.**—Within *Prosopigastra*, the lack of a ventral preapical expansion in the mandible is shared only by *morogoro* and *capensis* Brauns, and is clearly derived within the genus. The markedly modified male mesopleuron of *morogoro*, another conspicuous apomorphy, is also found in *capensis* and *creon* (Nurse). Most likely it is an independent development in the latter species, which belongs to the *globiceps* group of Pulawski (1979). The group is

characterized by the yellow legs markings and holoptic eyes in most males, two derived features that are absent in both *capensis* and *morogoro*. Thus, *capensis* and *morogoro* appear to be the closest relatives within *Prosopigastra*.

**Type material.**—Holotype ♂: Tanzania: Morogoro Region: 48 km W Morogoro at  $6^{\circ}56.9' S$   $37^{\circ}20.2' E$ , M.H. Bourbin and W.J. Pulawski (California Academy of Sciences). Paratypes (all in California Academy of Sciences): TANZANIA: Iringa Region: 18 km W Iringa at  $7^{\circ}53.8' S$   $35^{\circ}35.7' E$ , M.H. Bourbin and W.J. Pulawski, 9 June 2001 (1♂), 20 June 2001 (1♀, 5♂). Morogoro Region: same data as holotype: 3 June 2001 (2♂), 6 June 2001 (2♂), 11 June 2001 (2♂), 18 June 2001 (1♂); Omari S Haji and W.J. Pulawski, 2–3 July 2001 (1♂), 7 July 2001 (1♂), and 23 July 2001 (1♂). Most of the paratypes are deposited at the California Academy of Sciences, and one each in the Museum für Naturkunde, Berlin, The Natural History Museum, London, and the United States National Museum of Natural History, Washington, D.C.

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## A New Species of *Copidosoma* Ratzeburg (Hymenoptera: Encyrtidae) from Eagle Nests in Kazakhstan

ANDREY SHARKOV, TODD E. KATZNER, AND TATYANA BRAGINA

(AS) Department of Biochemistry, Chemical Abstracts Service, 2540 Olentangy River Road, Columbus, OH 43202, USA, email: asharkov2@cas.org;

(TEK) Department of Biology, Arizona State University, P.O. Box 871501, Tempe, AZ 85287-1501, USA;

(TB) Department of Biology, Kostanay State University, 118 Taran St., Kostanay, 458000, Kazakhstan

**Abstract.**—A new species of polyembryonic encyrtid of the genus *Copidosoma* is described from north-central Kazakhstan. *Copidosoma naurzumense*, n. sp., was reared from tineid moth larvae collected from regurgitated pellets collected near eagle nests in the Naurzum nature reserve. This is the third species of the genus *Copidosoma* reported from Kazakhstan. This species is similar to *C. longiventre* Myartseva from Turkmenistan, from which it differs by having dark tegulae and front coxae, shorter antennal segments and clava, and smaller body size. The natural history and ecology of the parasitoid and its host are discussed.

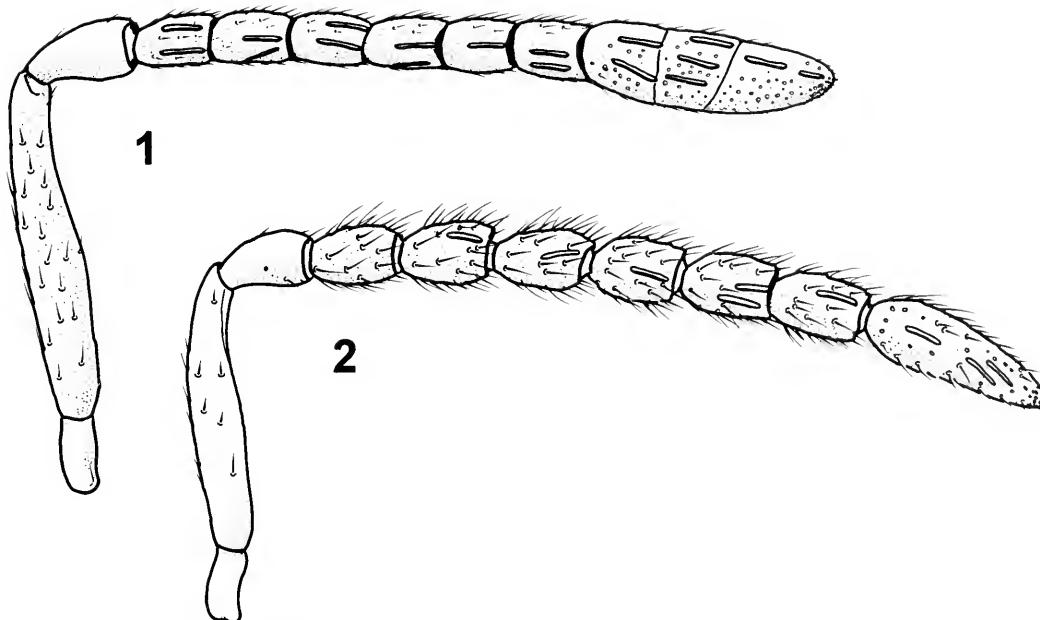
**Резюме.** — Описан новый вид энциртид рода *Copidosoma* из Казахстана (Наурзумский государственный природный заповедник). *Copidosoma naurzumense*, sp. n. выведен из гусениц молей семейства *Tineidae* (Lepidoptera), найденных в погадках, собранных около гнезд орлов. Это третий представитель рода *Copidosoma*, обнаруженный в Казахстане. *C. naurzumense* sp. n. сходен с *C. longiventre* Myartseva из Туркменистана, от которого он отличается темными тегулами и передними тазиками, более короткими члениками и булавой усиков, а также меньшими размерами тела. Приведены краткие сведения по биологии и экологии паразитоида и хозяина.

Parasitic wasps of the encyrtid genus *Copidosoma* are polyembryonic parasitoids of lepidopteran caterpillars. The genus has a worldwide distribution and, according to Noyes et al. (1997), includes about 150 described species. However, Trjapitzin (1989) suggests that there are 184 described species of *Copidosoma* in the world, 133 of which occur in the Palearctic. The fauna of the family Encyrtidae of Central Asia was revised most recently by Myartseva (1984), and includes 31 species of *Copidosoma* (4 of them as *Litomastix*), with only two species, *C. filicornis* (Dalman) and *C. longiventris* Ratzeburg, found in Kazakhstan.

The new species described below was reared by T. Katzner from caterpillars of clothes moths (Lepidoptera: Tineidae) collected from regurgitated pellets from eagles in the *Naurzumskiy Zapovednik* (Naurzum National Nature Reserve) in the Naurzumskiy region of the Kostanay Oblast' of north-central Kazakhstan (51° N, 64° E).

### *Copidosoma naurzumense* Sharkov, Katzner and Bragina

**Female.**—Body length 1.2–1.6 mm (holotype—1.44 mm). **Head:** Width approximately twice its length and equal to its height (35:18:35). Frontovertex width at



Figs. 1-2. *Copidosoma naurzumense* Sharkov, Katzner and Bragina, n. sp. 1—female antenna; 2—male antenna.

the level of anterior ocellus approximately  $\frac{1}{2}$  head width (18:35). Distance between posterior margin of eye and occipital margin approximately 1/9 eye length from above (1.5:13.5). Ocelli in obtuse triangle with the angle at the anterior ocellus of 103°. POL:OOL:LOL:OCL = 11:1.3:5.5:1. Maximum diameter of eye 1.2 times its minimum diameter (17:14). Distance between antennal toruli twice the distance between antennal torulus and mouth margin and approximately  $\frac{1}{3}$  the distance between antennal torulus and eye margin (4:2:13). Antenna as in Fig. 1. Mouth width slightly greater than malar space (16:15). Mesosoma: length 1.4 times its width (49:35). Scutum transverse, its length about  $\frac{2}{3}$  its width (22:35). Scutellum of equal length and width (22:22). Mid tibial spur length equal to length of first tarsomere (9:9) and approximately  $\frac{1}{4}$  length of middle tibia (9:35). Fore wing length 2.3 times its width (93:41) (Fig. 3). Metasoma: Longer than head and mesosoma combined. In dry specimens its length varies depending on degree of extension of sclerites, and

ranges from 1.1 to 2.0 times combined length of head and mesosoma (85:60 in the holotype). Ovipositor not exserted, with gonostyli fused to second valvifers, their length about  $\frac{1}{3}$  length of mid tibia. Color: Head and body generally dark, almost black. Face very dark brown, almost black, frons and vertex black, with very slight dark blue-green shine. Antenna dark brown, with slightly lighter apex of the pedicel. Scutum black, with dark blue-green shine, which is slightly more strongly expressed than on vertex; scutellum with slight dark purple reflection. All coxae dark brown. Front femur and tibia dark brown, with very light brown apex of femur and base of tibia, tibia very slightly lighter towards the apex; tarsus brown. Middle femur dark brown, with light brown apex; tibia light brown, with white translucent base, and gradually becoming brownish yellowish white toward apex; spur and tarsus almost white, with last tarsomere brownish. Hind femur dark brown, with light apex, tibia with whitish translucent base, dark brown in middle,

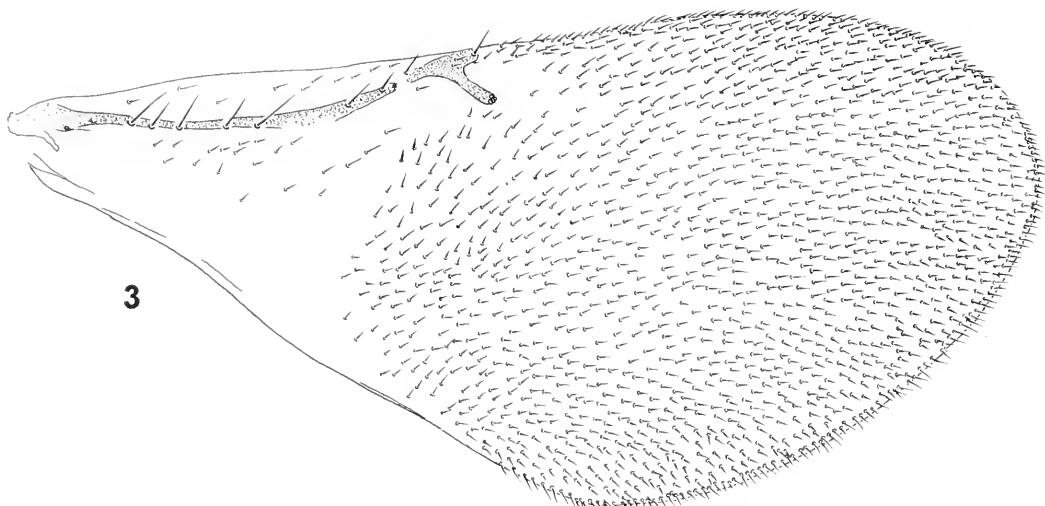


Fig. 3. *Copidosoma naurzumense* Sharkov, Katzner and Bragina, n. sp. female forewing.

and gradually becoming brownish yellow in apical  $\frac{1}{3}$ ; tarsus yellowish white, with last tarsomere brownish. Metasoma black, with very slight metallic reflection. *Sculpture*: Head and body reticulate, with cells rounded on frons, vertex, and dorsal side of mesosoma, and elongate on gena, mesopleuron and metasoma. Cell diameter on dorsal side of head and mesosoma about  $\frac{1}{2}$  diameter of posterior ocellus.

*Male*.—Body length 1.2–1.4 mm. General appearance as in female, except head slightly wider (width 2.1 times length and 1.1 times height), ocelli in more obtuse triangle (angle at anterior ocellus 115°), mid tibial spur slightly shorter than first tarsomere, and metasoma equal in length or shorter than head and mesosoma combined. Length of aedeagus, when exserted,  $\frac{1}{3}$  to  $\frac{1}{2}$  length of mid tibia. Digits with two teeth. Antenna as in Fig. 2. Color and sculpture as in female, although sculpture patterns somewhat more pronounced.

*Types*.—Holotype female: 51°33.3'N 064°07.9'E KAZAKHSTAN, Kostanay region, Naurzumskiy zapovednik, near Karantandy (formerly Dokuchaevka), eagle nest from nest #10, 6.v.1998, emerged 998 (Katzner). Paratypes: 2 females, 3 males, same data ex-

cept, 16.vii.1998; 30 males, same data except, eagle pellet from nest #21, 26.v.1999; 8 females, same data except, eagle pellet from nest #13, 26.V.1999; 3 females, 4 males, same data except, eagle pellet from nest #12, 19.vi.1999; 41 females, 43 males, same locality, summer 1998 (deposited at the OSU Insect Collection, Columbus, OH).

*Diagnosis*.—From *C. filicornis*, which also occurs in Kazakhstan, differs in having the metasoma longer than the head and mesosoma combined, and dark brown front coxa. The second species occurring in Kazakhstan, *C. bouchenii*, has white tegulae, the clava shorter than three preceding funicular segments, and the body length of 3.0–3.2 mm. In Myartseva's (1984) key runs to *C. longiventris* Myartseva from Turkmenistan, from which it differs by having dark tegulae and front coxae, shorter funicular segments and clava, and a smaller body size. In *C. longiventris* funicular segments are more than twice longer than wide, clava is equal in length to four preceding funicular segments combined, and the body length is 2.4 mm. In Trjapitzin's (1989) key *C. naurzumense* runs to *C. clavatum* Myartseva from Turkmenistan, from which, according to

Myartseva's (1984) key, it differs in having the metasoma longer than the head and mesosoma combined. In Kazmi and Hayat's (1998) key to Indian *Copidosoma*, runs to *C. kochleri*, an introduced South American species, which is a parasitoid of the potato tuber moth.

**Natural history and ecology.**—The climate in the region of the Naurzumskiy Zapovednik is harsh continental. Minimum winter temperatures are  $-45^{\circ}\text{C}$ , and summer maximums reach  $41^{\circ}\text{C}$ , with average yearly temperature being  $2.4^{\circ}\text{C}$ . Precipitation is highly variable, but averages 233 mm per year.

Parasitized and unparasitized host larvae were found in summers 1997–2000 in regurgitated pellets collected from nests and roosts of several species of eagles *Aquila* and *Haliaeetus*. Although hosts and parasitoids were collected from pellets during each month of the summer and late spring, host larvae were most frequently observed during the colder and wetter months of April and May. Host larvae were found in pellets composed of mammal fur, bird feathers, or mixtures of both. Of more than 9500 pellets evaluated, less than 500 contained the host larvae, with the number of larvae per pellet being generally less than ten, but occasionally more than 100. Current estimates of the parasitism rate are that it is less than 40%. Sterile defender (precocious) larvae occur in this species, as they do in several other polyembryonic encyrtids (Cruz 1981, 1986).

Similar numbers of tineid moths and hymenopterans were found in pellets of raptors in North America (Philips and Dindal 1979). Pellets represent a large concentration of potential food that can support diverse invertebrate communities.

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## Food Plants and Life Histories of Sawflies of the Families Tenthredinidae and Pergidae (Hymenoptera) in Costa Rica, with Descriptions of Four New Species

DAVID R. SMITH AND DANIEL H. JANZEN

(DRS) Systematic Entomology Laboratory, PSI, Agricultural Research Service,

U.S. Department of Agriculture, c/o National Museum of Natural History,

Smithsonian Institution, Washington, DC 20560-0168, USA, email: dsmith@sel.barc.usda.gov;

(DHJ) Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA,

email: djanzen@sas.upenn.edu

**Abstract.**—Food plants and biological information are given for five species of Tenthredinidae and six species of Pergidae reared in the Área de Conservación Guanacaste, Guanacaste Province, northwestern Costa Rica. The Tenthredinidae are *Adiaclema chigiyae* Smith, n. sp. on *Entodon-topsis leucostega* (Stereophyllaceae), *Waldheimia fascipennis* (Norton) on *Cissus pseudosicyoides* (Vitaceae), *Waldheimia suturalis* (Cameron) on *Cissus rhombifolia* (Vitaceae), *Waldheimia interstitialis* (Cameron), n. comb., on *Hamelia patens* (Rubiaceae), and *Pristiphora auricauda* Smith on *Prunus annularis* (Rosaceae). The Pergidae are *Aulacomerus daktus* Smith on *Mesechites trifida* (Apocynaceae), *Anathulea bimaculata* (Cameron) on *Hippocratea volubilis* (Hippocrateaceae), *Suwatnus nigriceps* (Cameron) on *Psidium guajava* (Myrtaceae), *Acordulecera binelli* Smith, n. sp., on *Posoqueria latifolia* (Rubiaceae), *Acordulecera liami* Smith, n. sp., on *Erythroxylum havanense* (Erythroxylaceae), and *Acordulecera dashielli* Smith, n. sp., on *Arrabidaea patellifera* (Bigoniaceae). Several hundred wild-caught larvae of these 11 species produced no parasitoids. Redescriptions are given for *Aulacomerus daktus*, *Anathulea bimaculata*, and *Suwatnus nigriceps*.

This is the second of two treatments of the host plants and life histories of sawflies reared by DHJ during the Lepidoptera caterpillar inventory of the Área de Conservación Guanacaste (ACG), which lies primarily in Guanacaste Province in northwestern Costa Rica. The first covered the family Argidae (Smith and Janzen 2003). Here we consider the families Tenthredinidae and Pergidae, the adults of which may be distinguished in the key to families by Smith (1988, 1995). Symphyta larvae are keyed to family and to subfamilies within the Tenthredinidae by Smith and Middlekauff (1987). Though based on the Nearctic fauna, this larval key will be helpful for larvae collected in Costa Rica. Details of the methods and rearing records may be found at <http://janzen.sas.upenn.edu> and in Janzen (2000, in press), Schauff

and Janzen (2001), Janzen et al. (2003), and Burns and Janzen (2001).

Acronyms used are: INBio = Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; BMNH = The Natural History Museum, London, UK. Voucher numbers associated with each reared adult are expressed as, for example, “99-SRNP-4547”; full details of the voucher record and associated images may be obtained at <http://janzen.sas.upenn.edu>.

### TENTHREDINIDAE

This is a large family in the Neotropics, with about 32 genera and over 300 species. Four of the six Neotropical subfamilies are known from Costa Rica, the largest being

the Selandriinae and Blennocampinae. Only a few species of the other two, Nematinae (Smith 2003a) and Allantinae (Smith 2003b), occur there. The subfamilies may be distinguished with the keys in Smith (1995, 2003a). All Tenthredinidae in Costa Rica have 9-segmented, filiform or slightly compressed antennae.

### SELANDRIINAE

This subfamily is recognized by its distinctive wing venation; most have vein 2A+3A complete, lack the anal crossvein, and have vein  $Rs+M$  distinctly curved near  $Sc+R$  in the forewing. It is the largest subfamily of Tenthredinidae in the Neotropics, and probably 60–70 species in nine genera occur in Costa Rica. Food plants are known for very few of them. Most extra-tropical members of this subfamily have ferns and grasses as food plants.

#### *Adiaclema* Enderlein

About 30 species of *Adiaclema* occur from southern Mexico to northern Argentina. The genus is distinguished by the absence of the anal crossvein in the forewing (a characteristic of the subfamily) and simple mandibles, a trait not possessed by other Neotropical Selandriinae. All other Neotropical selandriines have one or more subapical teeth on one or both mandibles. Types of all described species have been examined by DRS except for several that cannot be located, and it was determined that the following species reared in Costa Rica represents a new species. This is the first food plant record for the genus.

#### *Adiaclema chigiyae* Smith, new species

(Figs. 1, 8, 15, 16, 27, 32, 33, 37–39)

**Female.**—Length, 8.0–8.5 mm. Antenna black. Head black with clypeus, labrum, and maxillary and labial palpi white. Thorax orange. Abdomen orange with apical three segments and sheath black. Legs orange with foretarsal segments 3–4 slightly infuscate; midfemur with a narrow black

ring at apex; midtarsus black; apical  $\frac{2}{3}$  of hind tibia black with basal  $\frac{1}{3}$  white; hind tarsus black. Forewing yellow with apex beyond stigma black; costa, subcosta, stigma, and veins yellow in yellow area; veins black in black apex.

Antennal length  $2.1 \times$  head width; length of 3rd segment  $1.3 \times$  length of 4th segment; segments beyond third gradually decreasing in length (Fig. 8). Eyes large and converging below; lower interocular distance  $0.8 \times$  eye length; upper interocular distance slightly greater than eye length (Fig. 15). Head from above strongly narrowing behind eyes; postocellar area  $1.2 \times$  broader than long; distances between hind ocelli, hind ocellus and eye, and hind ocellus and posterior margin of head as 6:12:10 (Fig. 16). Malar space linear; clypeus with anterior margin slightly convex; labrum about  $2 \times$  broader than long with anterior margin truncate. Hind basitarsus subequal in length to length of remaining tarsal segments combined. Hind wing with anal cell sessile. Tarsal claw with long inner tooth slightly shorter than outer tooth and without basal lobe (Fig. 37). Sheath short and rounded at apex in lateral view; in dorsal view slightly broader at center (Fig. 32). Lancet (Fig. 27) short, triangular, with about 9 serrulae; protuberances laterally on annuli 2–10, becoming more spinelike toward apex.

**Male.**—Length, 7.1–7.5 mm. Color similar to that of female except mesoprescutum blackish at center and nearly all hind tibia black with white only at extreme base. Tarsal claw with long, slender outer tooth and minute inner tooth (Fig. 38). Genitalia (Fig. 39) with harpe elongate and rounded at apex; parapenis narrow, tapering to small rounded apex; apex of penis valve about as long as broad, rounded at apex, with long dorsal lobe.

**Holotype.**—Female, labeled "Voucher: D. H. Janzen & W. Hallwachs, caterpillar (Lepidoptera) database, Area de Conservacion Guanacaste, Costa Rica. <http://>

janzen.sas.upenn.edu, 99-SRNP.9777." Deposited at INBio.

**Paratypes.**—COSTA RICA: All labeled as holotype except for voucher codes: 99-SRNP-9757 (1♀); 99-SRNP-10267 (1♂); 99-SRNP-10269 (1♀); 99-SRNP-10273 (1♀); 99-SRNP-10285 (1♀); 99-SRNP-10288 (1♂); 99-SRNP-10297 (1♀); 99-SRNP-10305 (1♀); 99-SRNP-10314 (1♀); 99-SRNP-10334 (1♂); 99-SRNP-10348 (1♀); Guanacaste Province, Santa Rosa National Park, D. H. Janzen, 24-VIII-14-IX-1985, Malaise trap SE-6-C (1♀). Deposited at INBio and USNM.

**Etymology.**—This species is named in honor of Chigiy Binell in recognition of her great enthusiasm for the ACG and support for the Rincon Rainforest.

**Food plant and biology.**—Larvae (Fig. 1) feed on moss, *Entodontopsis leucostegia* (Brid.) W. R. Buck & Ireland (Stereophyllaceae). In the second month of the rainy season (late June to early July), the penultimate and last instar larvae were encountered feeding solitarily day and night while fully exposed on the rough surface of moss patches on logs and stumps in the ACG dry forest. They were not encountered in the first two decades of the caterpillar inventory because it did not occur to us to search shady, wet patches of moss.

The prepupal larva chews into the surface of rotten bark or wood, hollows out a smooth-walled ovoid chamber in which to pupate, and closes the entrance hole with wood or bark chips glued together. There is no sign of a silken cocoon in the chamber. The adult emerges 40–60 days after the cocooning chamber is constructed (average 47 days,  $n = 12$ ) in the ACG rainy season climate. There was no evidence of pupal dormancy, but this does not exclude the possibility that the prepupae or pupae late in the rainy season pass the six month dry season dormant in the cocoon chamber. No parasitoids were produced from 135 wild-caught penultimate and last-instar larvae.

**Remarks.**—Of the Neotropical *Adiaclema*

species, only a few have the combination of yellow wings with a black apex, black head, entirely orange thorax, and orange abdomen with the apical segments black. This color is similar to *Adiaclema tetricum* (Konow) described from "Peru (Pozuzo)" (type examined), but *A. tetricum* differs by having the supraclypeal area and area around antennal bases white, has much longer antennae (length nearly three times the head width), has a long, narrow ovipositor sheath (with valvula 3 about two times longer than broad), has the lower interocular distance about  $0.9 \times$  the eye length, and is generally larger, being about 10 mm in length. *Adiaclema blandulum* (Enderlein) (type not located) described from Ecuador is also similar, but has most of the face above the antennae white.

In all other *Adiaclema* species examined, the tarsal claws of the female and male are similar with a long inner tooth and without a basal lobe (Fig. 37). It is most unusual for the male tarsal claws to differ so much from those of the female (Figs. 37, 38).

#### BLENNOCAMPINAE

There are about 150 species in 14 genera of Blennocampinae in the Neotropical Region and 25–30 species in five genera in Costa Rica, most of which are in the large genus *Waldheimia*. The subfamily is distinguished by its wing venation, with veins M and 1m-cu parallel, veins M and Rs+M meeting Sc+R at the same point, and the anal cell petiolate with the basal section of vein 2A+3A absent. One species, *Metapediodes subcoerulea* (Cameron) has been reared from *Conostegia xalapensis* D. Don (Melastomataceae) (Smith 1995). Species of the genus *Periclista* Konow are found at high elevations in Costa Rica and may feed on *Quercus* sp. (Fagaceae), as do the North American counterparts.

#### *Waldheimia* Brullé

Nearly 100 species of *Waldheimia* are known with about ten in Costa Rica, and

the genus is widely distributed from southwestern United States to northern Argentina. Characteristics of the genus include the reduced apical four antennal segments, straight forewing vein 2A+3A, and the bifid tarsal claws with the inner tooth usually broader and longer than the outer tooth and with a basal lobe. Three species have been reared in ACG.

***Waldheimia fascipennis* (Norton)**  
(Fig. 2)

**Discussion.**—This is one of the few species of *Waldheimia* that have the forewings broadly black at both the base and apex and yellow in the center. The head, thorax, and abdomen are orange with the intercellular area, apical three abdominal segments, and sheath black. The coxae, trochanters, and femora are orange, the tibiae are white at the bases with the apical half to two-thirds black, the basitarsi are white with a narrow black apical ring, and the remaining tarsal segments are black. The male is unknown.

**Distribution.**—Costa Rica (Guanacaste); Mexico (Campeche, Chiapas); El Salvador. In addition to the reared specimens, the following from Costa Rica also have been examined: Santa Rosa National Park, 14-IX-5-X-1985, Malaise trap H-3-0; Prov. Guanacaste, OTS Palo Verde Sta., 29 km W.S.W. Canas, 10°21'N, 85°21'W, 14-VII-1976.

**Food plant and biology.**—*Waldheimia fascipennis* larvae feed on leaves of *Cissus pseudosicyoides* Croat (Vitaceae) during the rainy season in ACG dry forest (two females: 90-SRNP-1141, 83-SRNP-1144). One record from the last month of the rainy season represents either a second or third rainy season generation. The bluish and pale yellow larvae feed side-by-side on the upper sides of the relatively horizontal mature leaves in groups of 1-5 (Fig. 2). They are currently indistinguishable in color pattern, shape, and behavior to those of *Waldheimia suturalis*, which have been reared from *Cissus rhombifolia* in the same

habitat. Numerous *Waldheimia* larvae feeding on both species of *Cissus* have not produced adults, and it may be that both species of *Waldheimia* feed on both species of *Cissus*.

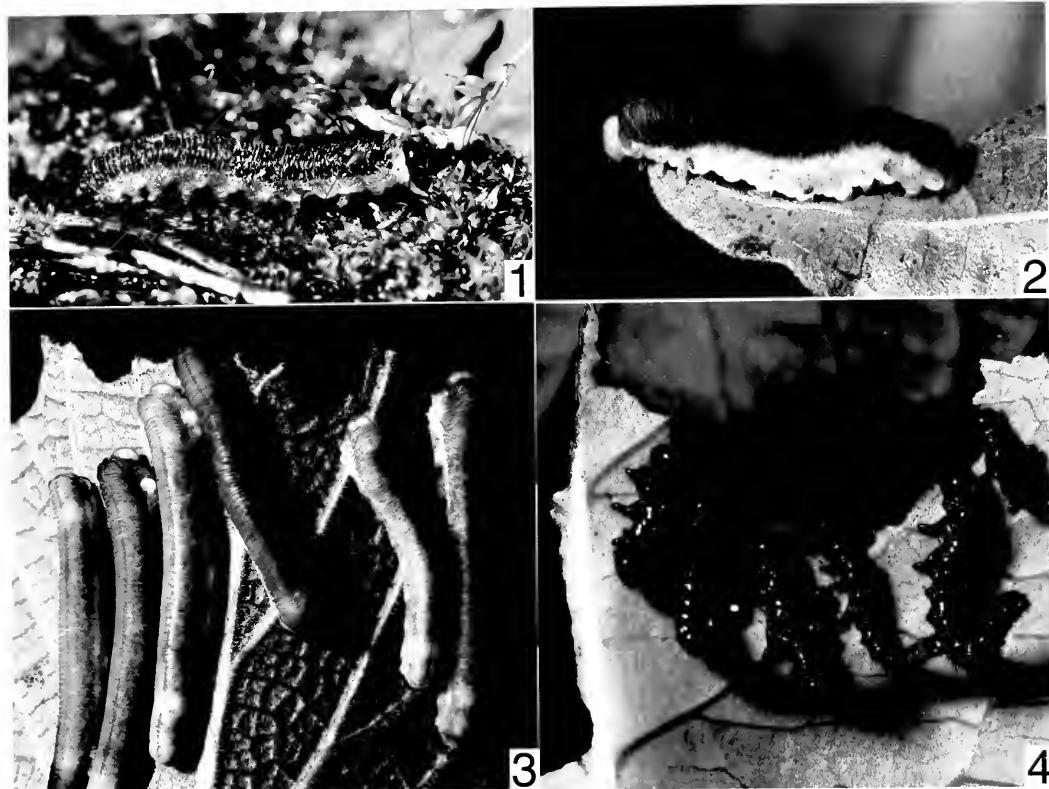
The prepupal larva burrows down into the litter and pupates naked in a chamber with no silk cocoon. The adults emerged 13-14 days after the prepupa entered the soil (n = 2). While no dormancy was recorded in rainy season pupae, the prepupae may well pass the dry season dormant in the litter. A total of 36 *Waldheimia* (*W. fascipennis* and *W. suturalis*) wild-caught penultimate and last-instar larvae produced no parasitoids.

***Waldheimia interstitialis* (Cameron),  
new combination**  
(Fig. 3)

**Discussion.**—This species was described in the genus *Blennocampa* Hartig by Cameron (1883) and transferred to *Erythraspides* Ashmead by Smith (in Kimsey and Smith 1985), but *Erythraspides* and *Waldheimia* cannot be distinguished in the Neotropics. Formal generic synonymy will be presented later in another paper, and here we give the new combination.

The coloration is distinctive for both sexes of this species. The antennae are black with the scape and pedicel orange. The head, thorax, and abdomen are orange with the intercellular area and sheath black. The legs are orange, with the apex of the midfemur, the entire hind femur, the apical third to half of the mid- and hind tibiae, and the apical three tarsal segments of all legs black. The wings are yellow with the apex beyond the stigma black. Cell M is absent in the hind wing.

**Distribution.**—Costa Rica (Alajuela, Guanacaste, Heredia, San José), Mexico (Veracruz); Panama; Venezuela. Costa Rican specimens examined are as follows: Prov. Heredia, La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N, 84°01'W, 6-VI-83, 27-IV-90, 17-I-91; Escazú, May 21, 24, 26, 27,



Figs. 1–4. Larvae. 1, *Adiaclema chigiyae*. 2, *Waldheimia fascipennis*. 3, *W. interstitialis*. 4, *Aulacomerus daktus*.

1987; Alajuela, 700 m, Penas Blancas, IV-1987.

**Food plant and biology.**—*Hamelia patens* Jacq. (Rubiaceae) was recorded as the host plant by Kimsey and Smith (1985) who also described and illustrated the larva and gave the life history in Panama. One female was reared from the same species of food plant in Costa Rica under number 00-SRNP-9451 (three others on the same food plant died of disease) in the lower margin of ACG cloud forest at about 1000 m elevation (April, July). *Waldheimia interstitialis* spun no cocoon, pupated naked in the bottom of its rearing container, and used eight days from prepupa until eclosion. The red-headed, dark gray-blue-black solitary larvae with the underside yellow (Fig. 3) are quite similar to those of the other two species of *Waldheimia* described here, and, like the others, feed in

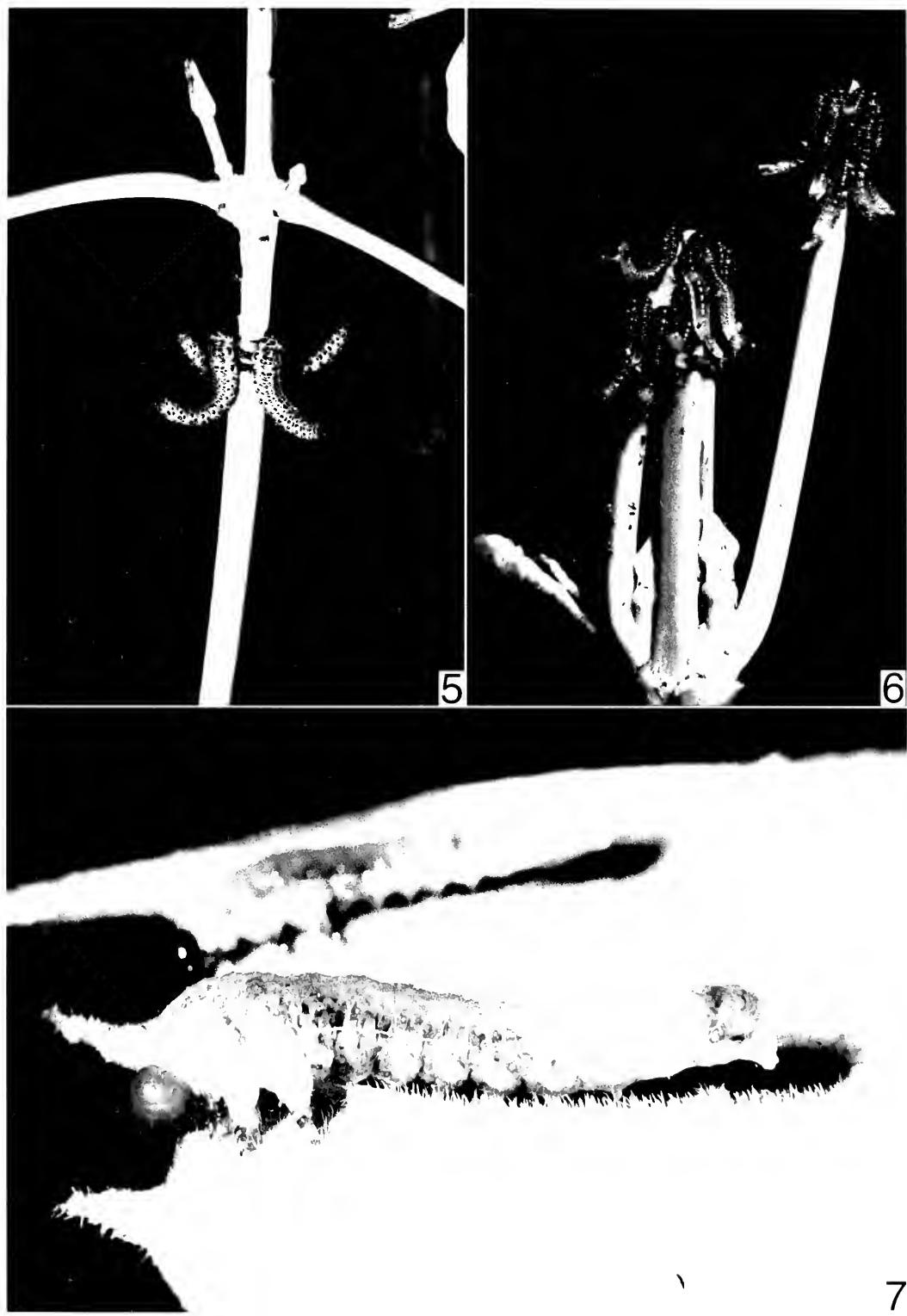
the daytime on the upper surface of the leaf.

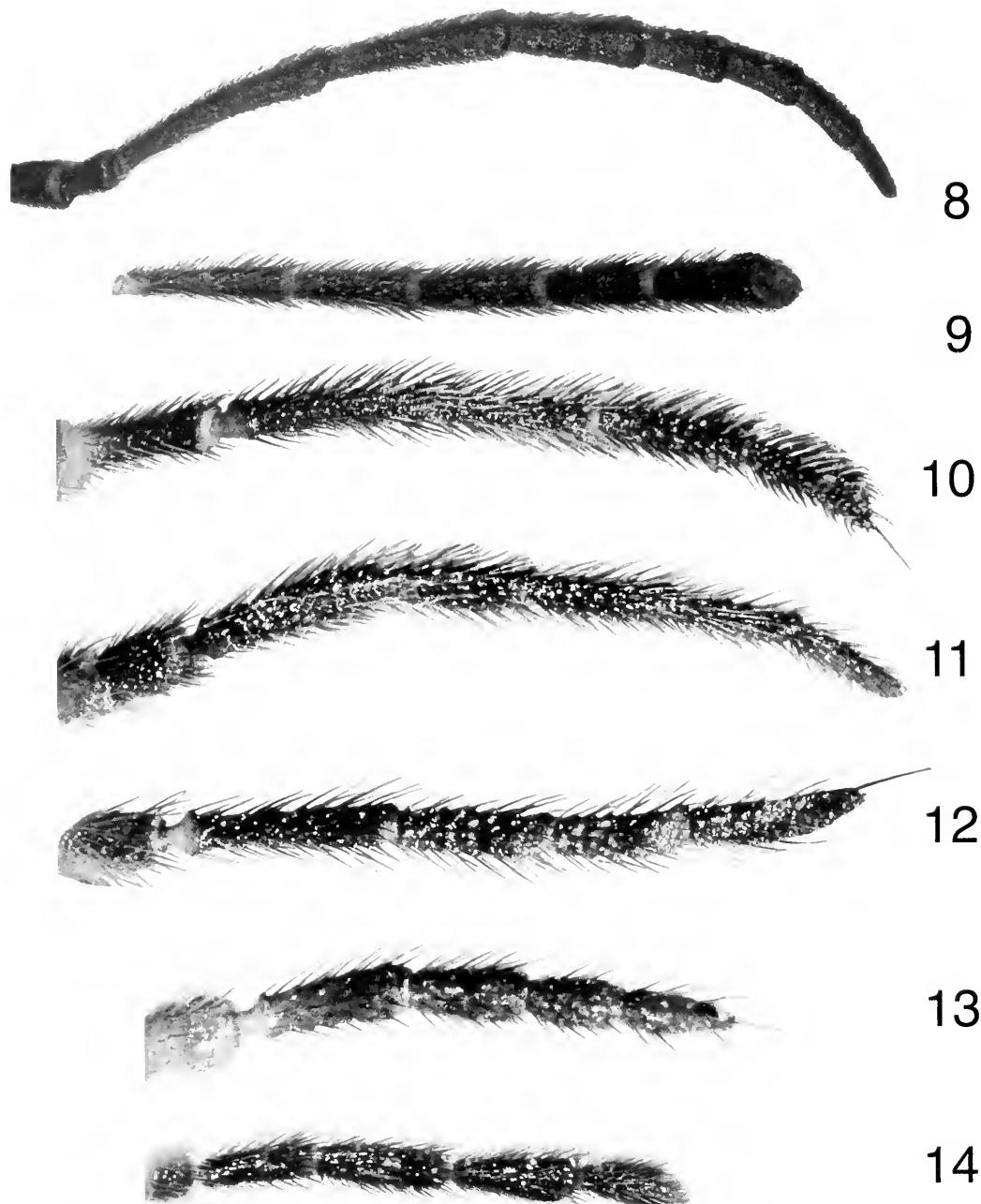
In laboratory rearings, Kimsey and Smith (1985), reported that the larvae go into the soil and form a smooth-walled, silk-lined cocoon. There were ten days from cocoon formation to eclosion.

#### *Waldheimia suturalis* (Cameron)

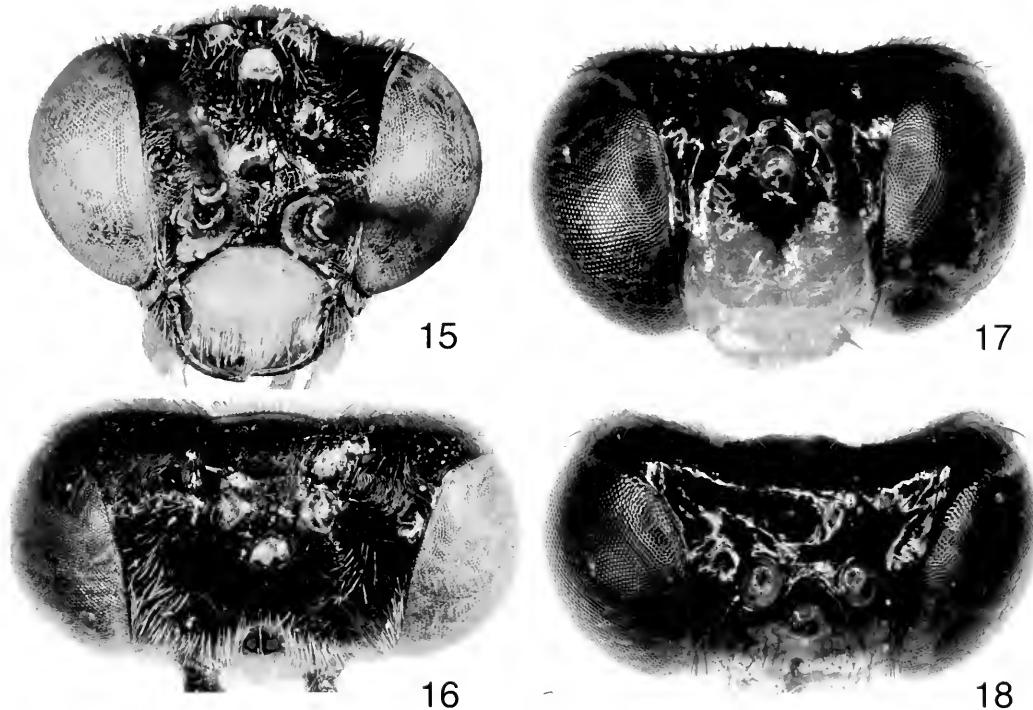
**Discussion.**—Both sexes of this species are entirely black with the following parts of the thorax red: pronotum, tegulae, mesonotum, mesopleuron, and upper half of the metapleuron. The wings are uniformly, darkly infuscated. The female has cell M present in the hind wing, and the male has a peripheral vein in the hind wing.

**Distribution.**—Costa Rica (Guanacaste, Heredia); Guatemala; Honduras; Mexico (Morelos, Veracruz). Specimens examined from Costa Rica other than those reared

Figs. 5-7. Larvae. 5, 6, *Amathalia bimaculata*. 7, *Acordulecerata dasielli*.



Figs. 8–14. Antennae. 8, *Adiaclema chigiyae*. 9, *Aulacomerus daktus*, flagellum. 10, *Anathulca bimaculata*. 11, *Suwatnus nigriceps*. 12, *Acordulecera binelli*, pedicel and flagellum. 13, *A. liami*, pedicel and flagellum. 14, *A. dashielli*, pedicel and flagellum.



Figs. 15–18. Head. 15, *Adiacleum chigiyae*, front view. 16, *A. chigiyae*, dorsal view. 17, *Anathulca bimaculata*, front view. 18, *A. bimaculata*, dorsal view.

are as follows: Guanacaste Prov., OTS Palo Verde Sta., 29 km W.S.W. Canas, 10°21'N, 85°21'W, 5-VII-1976; Heredia Prov., La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N, 84°01'W, 17-IV-1988.

**Food plant and biology.**—Three females were reared from larvae eating mature leaves of *Cissus rhombifolia* Vahl (Vitaceae) during the rainy season in ACG dry forest (83-SRNP-727, 98-SRNP-1831, and 98-SRNP-1833); two males were reared under numbers 98-SRNP-1832.1 and 98-SRNP-1832 from the same food plant species at the same time. The bluish and pale yellow larvae feed side-by-side on the upper sides of the relatively horizontal mature leaves in groups of one to five. They are currently indistinguishable in color pattern, shape, and behavior to those of *Waldheimia fascipennis*, which have been reared from *Cissus pseudosicyoides* in the same habitat. Numerous *Waldheimia* larvae feeding on both species of *Cissus* have not pro-

duced adults, and it may be that both species of *Waldheimia* feed on both species of *Cissus*.

The prepupal larva burrows down into the litter and pupates in a chamber with no silk cocoon. The adults emerged 56–102 days (average 74 days,  $n = 5$ ) after the prepupa entered the soil. This long pupation period is strikingly different from that of *W. fascipennis*, and probably represents some kind of rainy season dormancy. As mentioned above, a total of 36 *Waldheimia* (*W. fascipennis* and *W. suturalis*) wild-caught penultimate and last instar larvae produced no parasitoids.

#### NEMATINAE

This is a large subfamily in the arctic, subarctic, and temperate regions of the Northern Hemisphere. The number of species decreases sharply to the south, and very few are known from the Neotropics (Smith 2003a). *Pristiphora*, the only genus

known in Costa Rica, is the largest tropical-extending genus, and occurs from Mexico south to southeastern Brazil. The subfamily is recognized by its distinctive forewing venation, with veins M and 1m-cu markedly divergent, vein M meeting Sc+R far basal to the point where Rs+M meets Sc+R, and the anal cell petiolate with the base of vein 2A+3A absent.

### *Pristiphora* Latreille

More than 50 species are known in the Nearctic, but only nine are known from Mexico to southern Brazil, and three in Costa Rica, mostly from elevations above 1000 m. The Neotropical species are keyed and described in Smith (2003a).

#### *Pristiphora auricunda* Smith

**Discussion.**—The distinctive coloration of the female (antennae, thorax, and legs black, and abdomen a contrasting bright orange, except for black basal plates and black anterior margin of the second segment) distinguishes this species from other *Pristiphora* in Costa Rica. The male has the head, thorax, and legs mostly yellow orange, with most of the head and thorax dorsally and the tibiae and tarsi black. The abdomen is orange, as is that of the female. The female ovipositor and male genitalia are illustrated in Smith (2003a).

**Distribution.**—Costa Rica (Guanacaste). Other than the reared specimens from ACG, an additional Costa Rican record is from Est. Cacao, 1000–1400 m, Lado Sur-este del Volcan Cacao, Prov. Guan., II curso parataxon., Jun 1990.

**Food plant and biology.**—The larvae live solitarily in leaf rolls of mature leaves of *Prunus annularis* Koehne (Rosaceae). Fourteen females and seven males were reared from 60 leaf rolls collected from two trees in the lower edge of ACG cloud forest at about 1000 m elevation (00-SRNP-9074, -9075, -9077, -9100, -9107, -9112, -9114, -9121, -9122, -9123, -9124, -9125, -9126, -9127, -9128, -9130, -9131, -9132, -9133, -9134, -9135). Eleven to 30 days were used

between spinning the cocoon and eclosing (average 17 days, n = 14) during the relative warm weather of the dry season. There was no suggestion of dormancy. The cocoon is a rough dark brown shaggy cylinder spun directly on the surface of the green leaf in the rearing container, though in nature the larvae probably descend to the litter to spin their cocoons. No parasitoids were reared from 60 wild-caught larvae.

## PERGIDAE

Neotropical Pergidae were treated by Smith (1990). Eight subfamilies, 32 genera, and 256 species were recognized. Some additional species have been described since, and it would not be surprising if the number of described species is eventually doubled. Five subfamilies, ten genera, and 40 or more species occur in Costa Rica (Smith 1995). Representatives of two subfamilies, Loboceratiniae and Acorduleceriniae, have been reared by the ACG caterpillar inventory project.

Food plants for other species include jelly fungus (*Auricularia* sp.) growing on rotting wood for *Decameria rufiventris* (Cameron) (Perreyiinae) (Smith 1995) and dried leaves for *Perreyia tropica* (Norton) (Perreyiinae), the larvae of which travel in groups on the ground (Flores et al. 2000).

## LOBOCERATINAE

Three genera were treated by Smith (1990), but most species are in the genus *Aulacomerus*, which is the only Costa Rican genus. Two species were recorded from Costa Rica by Smith (1990), but more occur in the country. In Costa Rica, the subfamily is recognized by the 7-segmented, slightly clavate antennae with a large sensory pit on the apical segment, the midtibiae with a preapical spine, and the hind tibiae lacking a preapical spine.

### *Aulacomerus* Spinola

This genus contains 22 species and occurs from Mexico to northern Argentina



19



21



20



22

Figs. 19–22. Head. 19, *Suwatnus nigriceps*, front view. 20, *S. nigriceps*, dorsal view. 21, *Acordulecera binelli*, front view. 22, *A. binelli*, dorsal view.

(Smith 1990). This is the first food plant record for a member of this genus.

***Aulacomerus daktus* Smith**  
(Figs. 4, 9)

**Discussion.**—We redescribe this species since it was originally known from only a few specimens. It is distinguished from other *Aulacomerus* species by the key in Smith (1990).

**Description.**—Length of female, 8.5–9.5 mm; male 7.0–8.0 mm. Antenna black with scape and pedicel orange yellow. Head orange with ocellar area and postocellar area black and with light black markings toward antenna and sometimes from lateral ocellus to eye. Antennal tubercles, supraclypeal area, clypeus, labrum, and mandible whitish. Thorax orange. Legs orange with about apical half of hind tibia and all hind tarsus black; fore- and midtarsi black except bases of basitarsi usually orange yellow. Abdomen

orange with center of 6th tergum and segments 7 to apex and sheath entirely black. Wings yellow with apex beyond apex of stigma black; veins and stigma yellow, veins black in black apices.

Antennal length 1.6× head width; large sensory area on apical segment; 3rd segment slightly longer than 4th segment (Fig. 9). Clypeus with slight central circular emargination. Eyes slightly converging below, lower interocular distance subequal to eye length, upper interocular distance 1.1× eye length. Head from above narrowing behind eyes. Postocellar area 1.6× broader than long. Distances between hind ocelli, hind ocellus and eye, and from hind ocellus to posterior margin of head as 10:11:16. Hind basitarsus 1.3× length of remaining tarsal segments combined. Inner hind tibial spur 0.8× length of hind basitarsus. Female lancet and sheath and male genitalia illustrated by Smith (1990, figs. 338, 345, 368).

**Distribution.**—Costa Rica (Guanacaste), Guatemala, Mexico (Chiapas). This is the first record for Costa Rica. An additional record, other than the ACG specimens is: Vicinity Estac Murcielago, 8 km SW Cuajiniquil, Guanacaste Prov., 100 m, Jun 1989, GNP Biodiversity Survey 320300, 380200.

**Food plant and biology.**—Adults were reared from larvae eating mature leaves of *Mesechites trifida* (Jacq.) Müll. Arg. (Apocynaceae) [89-SRNP-500 (1♀); 92-SRNP-2490 (2♀, 1♂); 92-SRNP-3901 (3♀); 94-SRNP-9444 (5♀, 1♂); 94-SRNP-9529 (1♂)]. This species is occasionally encountered in groups of 3–7 greenish-black larvae (Fig. 4) feeding side-by-side on the upper or lower side of a single leaf of its herbaceous vine food plant during the mid to late rainy season in ACG dry forest. After consuming the entire leaf, the group moves up the stem to then consume the next leaf; in larval Lepidoptera, this has been interpreted as a strategy to remove the visual evidence of leaf damage from the view of avian predators (Heinrich 1993). As is commonplace with species of caterpillars feeding on latex-rich plants, the larvae cut the petiole of the leaf partly through before feeding on the blade, a behavior that reduces the flow of fresh latex from the bitten leaf blade (Dussourd and Eisner 1987). If the feeding group of penultimate or last-instar larvae is molested, they walk off in different directions on the food plant, but within an hour they regroup into the same feeding groups as before.

The penultimate instar larva molts into a non-feeding orange-purple morph that, in captivity, wanders on the foliage and litter for about 24 hours before spinning its smooth-walled, dark brown, ovoid cocoon in the litter. The adult emerges 12–16 days after cocoon spinning (average 14 days,  $n = 14$ ). A total of 28 wild-caught late instar larvae produced no parasitoids.

#### ACORDULECERINAE

This is a large subfamily with many undescribed species. Smith's (1990) key cov-

ers ten genera, four of which occur in Costa Rica (Smith 1995). Many are very small, no more than 3–4 mm in length. The antennae are 6–9 segmented, mostly 6-segmented and filiform, the eyes are large, occupying much of the head, the mid- and hind tibiae each have a preapical spine, and the hind wing usually has the veins forming the base cells RS and M in a straight or almost straight line. *Acordulecerinae*, as defined by Smith (1990), is by far the largest genus in this subfamily.

#### *Anathulea* Malaise

*Anathulea* is characterized by the 6-segmented antenna, truncate clypeus which is two times or more broader than long, and the long pedicel which is one and one-half times or more longer than broad and nearly as long as the first flagellar segment (Fig. 10). Four species were listed by Smith (1990) from Guatemala and Brazil, but 10 to 20 species probably occur in the Neotropics. This is the first food plant record for a member of this genus.

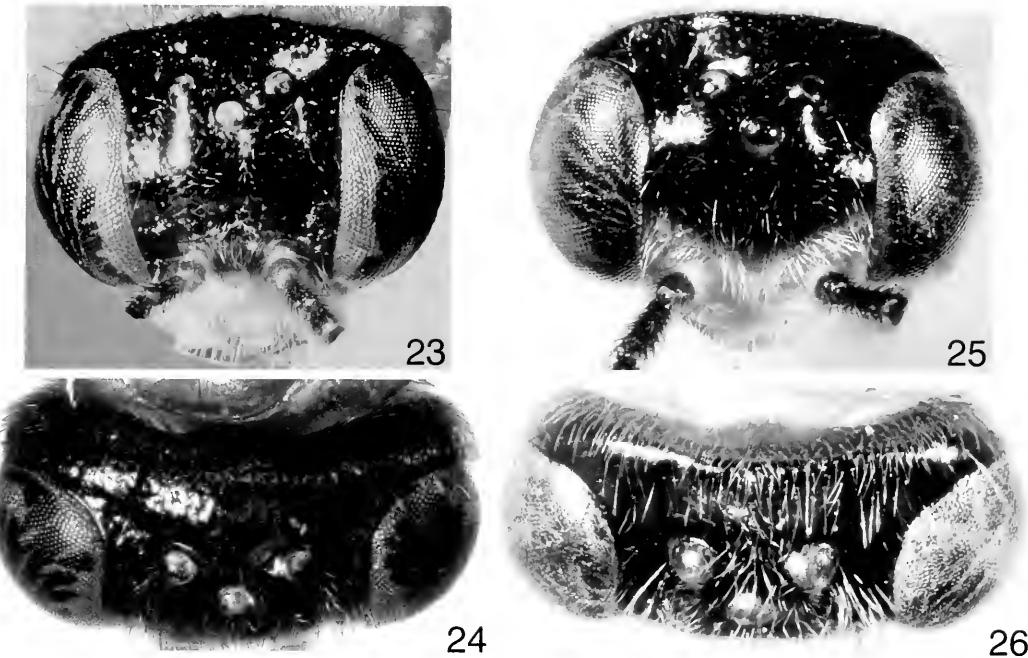
#### *Anathulea bimaculata* (Cameron)

(Figs. 5, 6, 10, 17, 18, 28, 33, 40)

**Discussion.**—This species has not been treated since its original description. It was described from Guatemala (Cameron 1883).

**Female.**—Length, 6.3–7.5 mm. Antenna black with scape and base of pedicel orange yellow. Head black, orange yellow from halfway between ocelli and antennae to clypeus and labrum. Thorax orange yellow with prescutum (except for sides) and lateral lobes (except for depressed lateral areas) black. Legs orange with apical 4 tarsal segments black. Abdomen orange with segments 7 or 8 to apex black. Forewing yellow, apex beyond apex of stigma black; veins and stigma yellow, veins black in black apex.

Antennal length 1.4× head width; pedicel 2.7× longer than broad and 0.6× length of 3rd segment, 3rd segment 1.5× length of 4th segment; long seta at apex of



Figs. 23–26. Head. 23, *A. liami*, front view. 24, *A. liami*, dorsal view. 25, *A. dashielli*, front view. 26, *A. dashielli*, dorsal view.

apical segment (Fig. 10). Eyes large and strongly converging below, lower interocular distance  $0.6 \times$  eye length, upper interocular distance  $0.9 \times$  eye length (Fig. 17). Head from above strongly narrowing behind eyes; postocellar area  $2.1 \times$  broader than long; distances between hind ocelli, hind ocellus to eye, and hind ocellus to hind margin of head as 7:6:8 (Fig. 18). Hind basitarsus  $1.2 \times$  longer than length of remaining tarsal segments combined; inner hind tibial spur  $0.6 \times$  length of hind basitarsus; hind tarsal segments 2–4 each as broad as long. Sheath (Fig. 33) long, length subequal to length of hind tibia; without scopae, in dorsal view broad, rounded to acute apex. Lancet (Fig. 28) with about 32 serrulae, broad at base and tapering to apex, with numerous, closely set annuli slanted toward apex dorsally.

**Male.**—Length, 4.8–6.0 mm. Similar to female except mesoprescutum mostly orange and costa and subcosta of forewing more brownish. Genitalia (Fig. 40) with harpe round, slightly broader than long,

with long hairs; parapenis acute on meson; penis valve rounded ventrally, slightly concave dorsally, without spines.

**Distribution.**—Costa Rica (Guanacaste), Guatemala, Panama. These are the first records for Costa Rica and Panama. In addition to the rearings from ACG, specimens from Costa Rica have been examined from the following: Est. Maritza, 600 m, Lado oeste Volcan Orosi, Prov. Guan., II curso Parataxonomos, Ago 1990, L-N-326900, 373000; Guanacaste, W side Volcan Orosi, Est. Maritza, 600 m, 1988; Guanacaste NP, riparian, Oct. 20, 1977; Guanacaste Prov., Santa Rosa National Park, D. H. Janzen, 11-V-1-VI-85, Malaise trap BH-9-0, 13-VII-3-VIII-85, Malaise trap BH-12-C, 16-XI-7-XII-85, Malaise trap BH-10-C, 24-VIII-14-IX-84, Malaise trap SE-5-0.

**Food plant and biology.**—The larvae feed on the new shoot tips and shoot epidermis of *Hippocratea volubilis* L. (Hippocrateaceae) in the ACG dry forest (20♀ and 10♂: 01-SRNP-15925 to -15983, 01-SRNP-15940

to -15945, 01-SRNP-15947 to -15949, 01-SRNP-15951 to -15953, and 01-SRNP-16144 to -16146). The gray-brown early instar larvae occur in a tight cluster of 8–12 larvae arrayed on the lengthening shoot tips (Figs. 5, 6) of vine shoots growing horizontally (in search of insulated areas) across the forest floor in the deep shade of old-growth forest in the second month (July) of the rainy season. In this position, the larvae are extremely cryptic, appearing to be a cluster of small leaf buds at the shoot tip end (possibly an example of collective mimicry; Pasteur 1982). The larvae collectively eat the very tender shoot tip back down the stem until reaching the woody stem, and then continue back down the stem eating off the green tender outer epidermis, leaving the dead beige woody branch end (Fig. 6). These later instar larvae, arranged 3–6 around the stem look like dead tissue peeling back from the stem. There is no sign of larvae in the canopy tens of meters above where the mature woody vines have their crowns in the full sun.

The prepupal larvae drop or crawl off into the litter and spin solitary beige-brown ovoid cocoons among the dead leaves. There are 14–20 days between cocoon spinning and adult eclosion (average 16 days,  $n = 31$ ). About 100 wild-caught larvae of all ages produced no parasitoids.

#### *Suwatnus* Smith

This genus is very similar to *Acorduleceria*, but has 7-segmented antennae (Fig. 11). One species was treated by Smith (1990).

#### *Suwatnus nigriceps* (Cameron) (Figs. 11, 19, 20)

*Discussion.*—We redescribe this species because the original description is not adequate. It was described from “Mexico” by Cameron (1883).

*Female.*—Length, 4.2–4.7 mm. Antenna black. Head black with clypeus and mouthparts yellow orange and apical

maxillary palpal segment blackish; apex of mandible reddish brown. Thorax orange; tegula black; upper part of mesopleuron may be blackish. Legs orange white with tarsi and outer surfaces of tibiae black. Abdomen orange ventrally and laterally, black above with central longitudinal orange stripe; sheath black. Wings lightly, uniformly infuscated; veins and stigma black.

Antennal length  $1.1 \times$  head width; 3rd segment  $0.8 \times$  length of 4th segment, flagellar segments each longer than broad; apical segment without a long seta (Fig. 11). Eyes strongly converging below, lower interocular distance  $0.8 \times$  eye length; upper interocular distance subequal to eye length (Fig. 19). Head from above strongly narrowing behind eyes; postocellar area  $2.0 \times$  broader than long; distances between hind ocelli, hind ocellus and eye, and hind ocellus and posterior margin of head as 11:8:19 (Fig. 20). Hind basitarsus  $1.3 \times$  longer than length of remaining tarsal segments combined. Sheath with slender, posteriorly projecting scopae; sheath and lancet illustrated by Smith (1990, figs. 415, 420).

*Male.*—Length, 4.3 mm. Black, with head similar to that of female; thorax black with pronotum brownish; legs white with bases of coxae, tarsi, and stripe on outer surface of mid- and hind femora black; abdomen black with paired brownish spots on terga 2–4. Genitalia illustrated by Smith (1988, fig. 418).

*Food plant and biology.*—Three females and one male were reared from larvae feeding on mature leaves of *Psidium guajava* L. (Myrtaceae) (99-SRNP-3146) on the ACG interface of dry forest with rainforest. The white, solitary, globular silk cocoons were spun among the litter in the rearing container. Six wild-caught larvae produced no parasitoids.

#### *Acorduleceria* Say

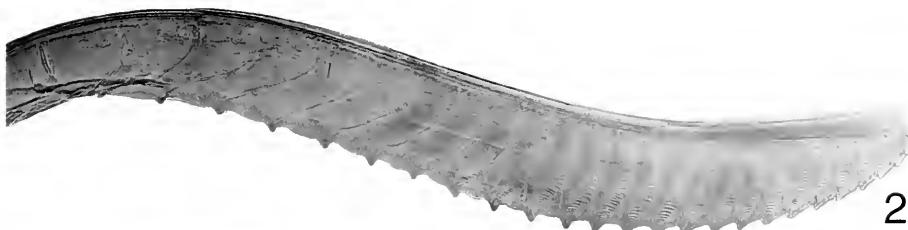
This large genus occurs from southern Canada to Argentina. Smith (1990) did not give a species key but listed the 45 de-



27



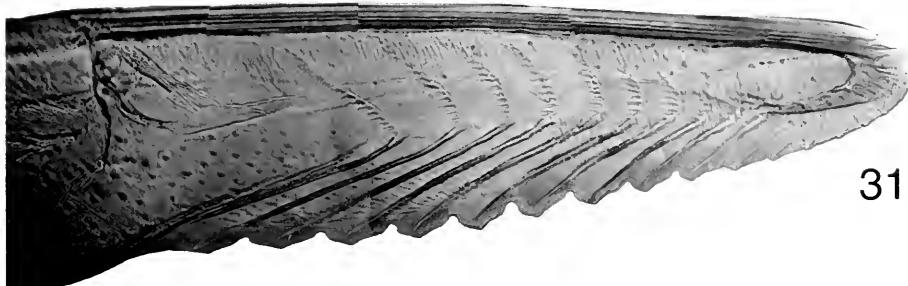
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31

Figs. 27–31. Female lancets. 27, *Adiaclema chigiyae*. 28, *Anathulea bimaculata*. 29, *Acordulecera binelli*. 30, *A. liami*. 31, *A. dashielli*.

scribed species from south of the United States. There are numerous undescribed species, and the size of the genus may exceed 200 species. Most species are small, 4–6 mm long, and all have 6-segmented antennae (Figs. 12–14). Probably more than 20 species occur in Costa Rica, most of which are undescribed. All types of the

Neotropical species have been examined by DRS; the following three species do not agree with the three described species from Mexico and Central America, and they are not the same as any of the species described from South America. Because of the new host plant and life history information, they are described here.

*Acordulecera binelli* Smith, new species  
(Figs. 12, 21, 22, 29, 34)

*Female*.—Length, 5.5 mm. Antenna black with scape orange yellow. Head black, yellow orange below line just in front of front ocellus (Fig. 21); mouthparts yellow orange; apex of mandible reddish brown. Thorax yellow orange with pronotum white and mesonotal front and lateral lobes, tegula, and metanotum black. Legs orange with apical three tarsal segments black. Abdomen and sheath orange. Wings uniformly hyaline; forewing with apical half of costa and stigma, except for black extreme apex, yellow orange, other veins black.

Antennal length  $1.1 \times$  head width and  $2.1 \times$  distance between eyes above; 3rd segment  $1.4 \times$  length of 4th segment; apical segment slightly longer than 4th segment and  $4.1 \times$  longer than broad; apical segment with long apical seta; hairs long, mostly longer than width of segments (Fig. 12). Head with scattered punctures. Eyes converging below, lower interocular distance about  $0.7 \times$  eye length; upper interocular distance about  $0.9 \times$  eye length (Fig. 21). Head from above strongly narrowing behind eyes; postocellar area about  $2.0 \times$  broader than long; distances between hind ocelli, hind ocellus and eye, and hind ocellus and posterior margin of head as 7:7:10 (Fig. 22). Distance between antennae subequal to distance between antenna and eye. Hind basitarsus  $1.4 \times$  length of remaining tarsal segments combined. Sheath (Fig. 34) with stout, short lateral scopae, in lateral view scopae rounded and about equal to length of inner portion of sheath, in dorsal view with long hairs slightly curved inward. Lancet (Fig. 29) long, with about 24 rounded serrulae, serrulae at apex flatter; annuli on apical half with hairs, annuli on basal half with no or only short, indistinct hairs.

*Male*.—Unknown.

*Holotype*.—Female, labeled “Voucher: D. H. Janzen & W. Hallwachs caterpillar

(Lepidoptera) database, Área de Conservación Guanacaste, Costa Rica, <http://janzen.sas.upenn.edu/>, “00-SRNP-9024.” Deposited at INBio.

*Etymology*.—This species is named in honor of Rich Binell in recognition of his great enthusiasm for the ACG, love of its roads, and support for the Rincon Rainforest.

*Food plant and biology*.—Three larvae were found feeding side-by-side on mature leaves of *Posoqueria latifolia* (Rudge) Roem. & Schult. (Rubiaceae) in lower ACG cloud forest at about 1000 m elevation. The larvae are yellowish at the rear and thorax, with a black head. Two died of disease and one spun a broadly ovoid, pinkish-beige cocoon directly on the surface of a leaf in the rearing container. The adult emerged 26 days later.

*Remarks*.—The color and presence of a seta on the apical antennal segment is quite similar to *Acordulecera lituratus* (Kownow) described from Amapá, Brazil. In *A. lituratus*, the abdomen is black above, and the apical seta of the apical antennal segment is extremely long, nearly as long as the apical antennal segment. Characters of the antenna, head, sheath, and lancet should be examined and compared with the illustrations for identification of this species.

*Acordulecera liami* Smith, new species  
(Figs. 13, 23, 24, 30, 35, 41)

*Female*.—Length, 4.1–4.4 mm. Antenna black, scape and pedicel more whitish. Head black with clypeus and mouthparts yellow orange; apex of mandible reddish brown. Thorax orange. Legs yellow orange with apical 2–3 segments of fore- and midtarsi and entire hind tarsus black. Abdomen orange, dorsally black with median, longitudinal orange stripe; sheath black. Wings hyaline; veins and stigma black.

Antennal length  $0.6 \times$  head width and  $1.2 \times$  distance between eyes from above; 3rd segment  $1.4 \times$  length of 4th segment;

apical segment subequal in length to 4th segment and  $2.8\times$  longer than broad at its greatest width; long seta at apex of apical segment; hairs equal to or longer than width of segments (Fig. 13). Head shining with scattered punctures. Eyes converging below, lower interocular distance  $0.8\times$  eye length; upper interocular distance subequal to eye length (Fig. 23). Head from above strongly narrowing behind eyes; postocellar area  $2.0\times$  broader than long; distances between hind ocelli, hind ocellus and eye, and hind ocellus and posterior margin of head as 10:7:10 (Fig. 24). Distance between antennae  $1.7\times$  distance between antenna and eye. Hind basitarsus subequal in length of length of remaining tarsal segments combined. Sheath (Fig. 35) with short, stout scopae, in lateral view scopa narrow and rounded, shorter than inner portion of sheath, in dorsal view with slightly incurved hairs. Lancet (Fig. 30) with about 14 pointed serrulae; annuli strongly slanted apically toward dorsum and lacking hairs or armature.

**Male.**—Length, 3.1 mm. Similar in color and structure to female except antenna with only scape whitish; thorax black with posterior margin of pronotum yellow orange with small spot at center of mesoscutellum orange; abdomen black with basal sterna pale orange and median longitudinal orange stripe only on anterior half of dorsum. Genitalia (Fig. 41) with harpes nearly rectangular, parapenis rounded mesally, and penis valve nearly straight ventrally, slightly concave dorsally, narrowly rounded at apex, and without spines.

**Holotype.**—Female, labeled "Voucher: D. H. Janzen & W. Hallwachs caterpillar (Lepidoptera) database, Área de Conservación Guanacaste, Costa Rica, <http://janzen.sas.upenn.edu>, 98-SRNP-1825." Deposited at INBio.

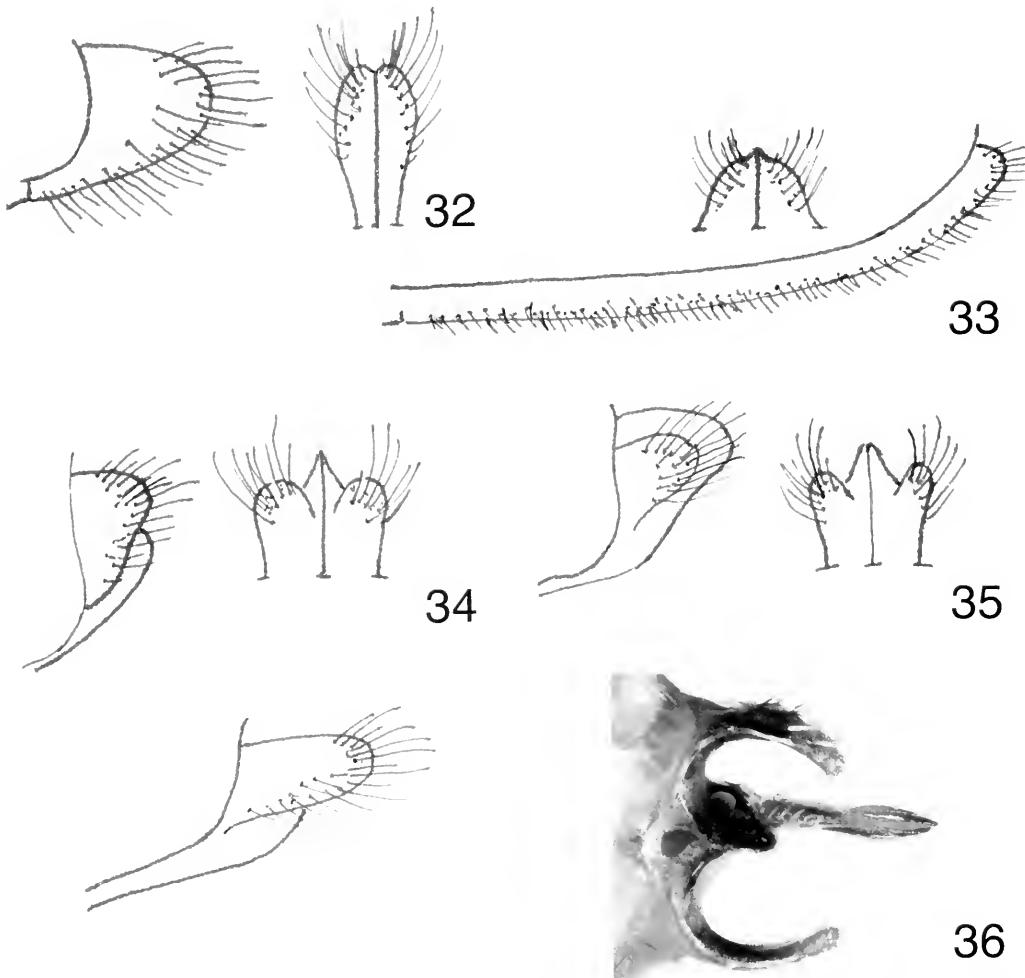
**Paratypes.**—COSTA RICA: Same labels as holotype, except numbers, 98-SRNP-1823 (1♀), 98-SRNP-1826 (1♀), 98-SRNP-1827 (1♀), 98-SRNP-1824 (1♂); Costa Rica,

Guanacaste Province, Santa Rosa National Park, D. H. Janzen, 11-V-1-VI-1985, Malaise trap SE-8-C (5♀), Malaise trap H-1-0 (1♀), Malaise trap SE-5-0 (1♀), Malaise trap H-2-C (1♀), Malaise trap SE-7-0 (3♀), Malaise trap SE-6-C (11♀), Malaise trap BH-9-0 (1♀); 1-22-VI-1985, Malaise trap SE-6-C (1♀). Deposited in INBio, USNM, BMNH.

**Etymology.**—This species is named in honor of Liam Binell in recognition of his great enthusiasm for the ACG, potential as crocodile bait, and support for the Rincon Rainforest.

**Food plant and biology.**—The light green larvae feed on the new and expanding leaves of the understory shrub *Erythroxylum havanense* Jacq. (Erythroxylaceae) in the first month of the rainy season in ACG dry forest. They feed solitarily, one on each of the small ovoid leaves, and perch along the margin so as to appear to be part of the leaf. In some years, such as 1992 and 1998, they were extremely abundant, nearly defoliating many of the food plant shrubs. The solitary beige to brown ovoid cocoons are spun among the litter. Only five days transpire between spinning and adult eclosion. No parasitoids were reared from hundreds of wild-caught larvae.

**Remarks.**—This species is close in color to *Acordulecera calceolatus* (Konow) described from Oyapock, Brazil, and *A. cervicatus* (Konow) described from Itaituba, Brazil, all sharing the presence of a long seta on the apical antennal segment. In *A. calceolatus*, the mesoprescutum and mesoscutellum are dark orange, the abdominal dorsum is black, the apical 2–3 tarsal segments are black, and the sheath has more slender, projecting lateral scopae. In *A. cervicatus*, the anterior half of the mesoprescutum, apical half of the mesoscutellum, and the metascutellum are black, the abdomen is orange with the apical two segments black, and the tibiae and tarsi are black. Identification of *A. liami* should be based on comparison of the specimens with the illustrations.



Figs. 32-36. Female sheaths, lateral and dorsal views. 32, *Adiaclema chigiyae*. 33, *Anathulea bimaculata*. 34, *Acordulecer a binelli*. 35, *A. liami*. 36, *A. dashielli*.

*Acordulecer a dashielli* Smith,  
new species

(Figs. 7, 14, 25, 26, 31, 36, 42)

*Female*.—Length, 4.8-5.2 mm. Antenna black with scape yellow orange. Head black with area below line just above antennae and mouthparts yellow orange (Fig. 25); apex of mandible reddish brown. Thorax orange with tegula black; blackish area laterally on each mesonotal lateral lobe. Legs orange with tibiae and tarsi black. Abdomen orange with apical two terga and sheath black. Wings moderately

and uniformly infuscated; veins and stigma black.

Antennal length subequal to head width and 1.9 $\times$  distance between eyes from above; 3rd segment slightly shorter than 4th segment; apical segment 0.8 $\times$  length of 4th segment and 2.5 $\times$  longer than broad at its greatest width; apical segment without long seta at apex; hairs equal to or shorter than width of segments (Fig. 14). Head shining, nearly impunctate. Inner margin of eyes subparallel, hardly converging below, lower and upper inter-

ocular distances subequal to slightly shorter than eye length (Fig. 25). Head from above strongly narrowing behind eyes; postocellar area 2.1× broader than long; distances between hind ocelli, hind ocellus and eye, and hind ocellus and posterior margin of head as 10:8:11 (Fig. 26). Distance between antennae 2.8× distance between antenna and eye. Hind basitarsus 1.3× longer than length of remaining tarsal segments combined. Sheath (Fig. 36) with long, narrow projecting scopae, in lateral view slender and rounded, much longer than inner portion of sheath; in dorsal view, scopae forcepslike, curving inward at apices. Lancet (Fig. 31) short, with about 14 serrulae, with slight dorsoapical notch at apex. Basal 8 serrulae broad and rounded and separated by narrow notch; serrulae beyond 8 small and becoming indistinct toward apex. Annuli strongly curved, ventral half without hairs, dorsal half with fine hairs.

**Male.**—Length, 3.5–4.2 mm. Similar to female except bases of tibiae paler and apical maxillary palpal segments blackish. Genitalia (Fig. 42) with harpe nearly triangular, lateral and apical margins rounded, inner margin straight; parapenis rounded mesally; penis valve elongate, rounded at apex, with ventral and lateral spines.

**Holotype.**—Female, labeled “Voucher: D. H. Janzen & W. Hallwachs caterpillar (Lepidoptera) database, Area de Conservación Guanacaste, Costa Rica, <http://janzen.sas.upenn.edu>, 96-SRNP-6815.” Deposited at INBio.

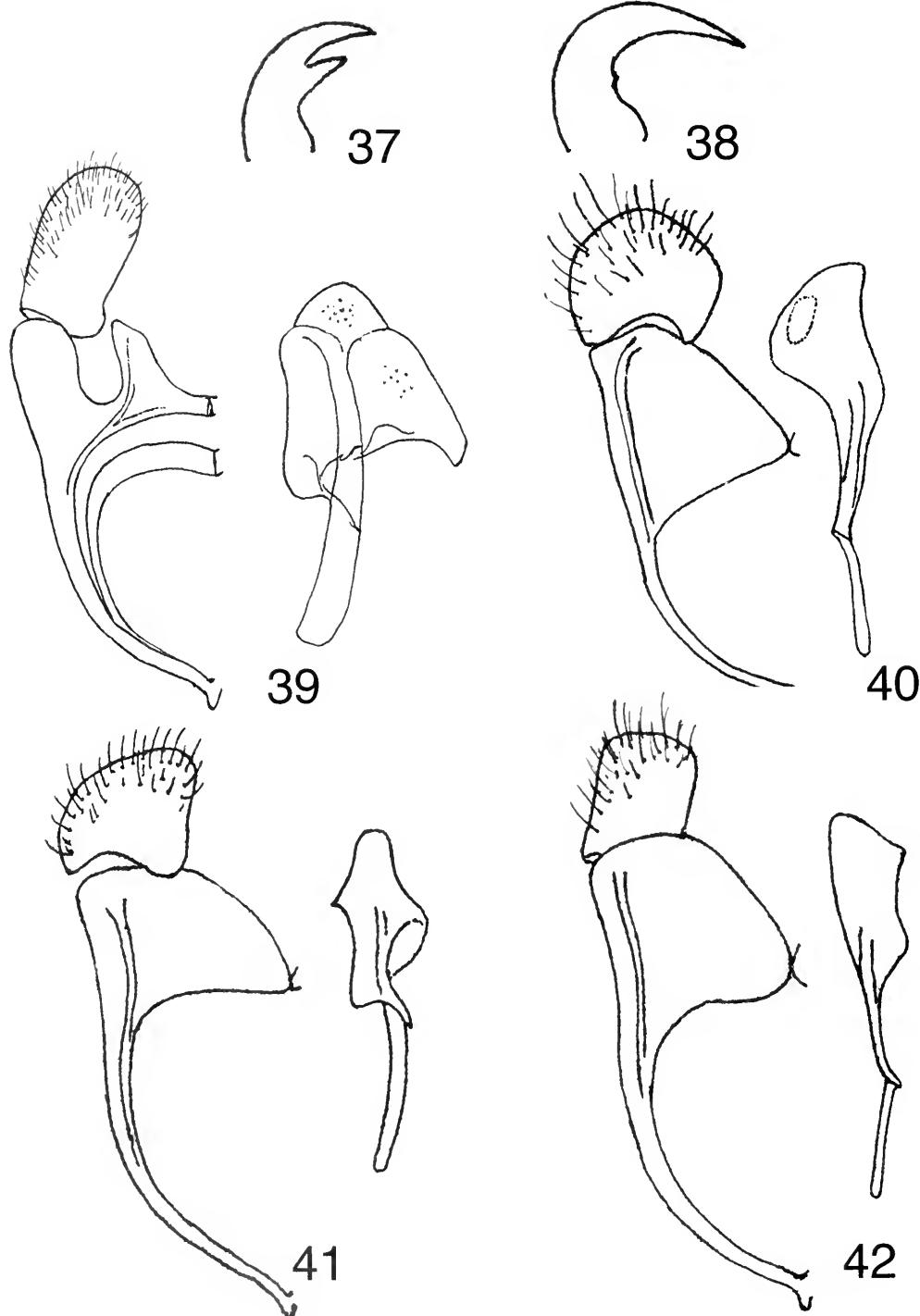
**Paratypes.**—COSTA RICA: Specimens labeled as above, all beginning with 96-SRNP-: 6811 (1♀); 6815 (1♀); 6821 (1♂); 6822 (1♂); 6824 (1♀); 6824.1 (1♀); 6825 (1♀); 6826 (1♀); 6829 (1♀); 6948 (1♀); 6948.1 (1♀); 6948.2 (1♀); 6948.3 (1♀); 6948.4 (1♀); 6948.5 (1♀); 6948.7 (1♀); 6948.8 (1♀); 6948.10 (1♀); 6948.11 (1♀); 6948.12 (1♀); 6948.13 (1♀); 6948.14 (1♀); 6948.15 (1♀); 6948.16 (1♀); 6948.17 (1♀); 6948.18 (1♀); 6948.19 (1♀); 6948.20 (1♀;

6948.21 (1♂); 6948.22 (1♂); 6948.23 (1♂); 6948.24 (1♀); 6948.25 (1♀); 6948.26 (1♀); 6948.27 (1♀); 6984.6 (1♀); 6984.9 (1♀); Guanacaste Province, Santa Rosa National Park, D. H. Janzen, 11-V-1-VII-1985, Malaise trap H-2-C (1♀), 11-V-1-VI-1985, Malaise trap SE-8-C (1♂), Malaise trap H-2-C (1♂), Malaise trap SE-7-0 (1♂), Malaise trap SE-6-C (3♂), 1-22-VI-1988, Malaise trap SE-8-C (1♀), 14-IX-5-X-1985, Malaise trap SE-7-0 (1♀), 22-VI-13-VII-1985, Malaise trap H-4-C (1♀). Deposited in INBio, USNM, BMNH.

**Etymology.**—This species is named in honor of Dashiell Binell in recognition of his great enthusiasm for the ACG, love of its beaches, and support for the Rincon Rainforest.

**Food plant and biology.**—The larvae feed on the newly expanded leaves of the wood vine *Arrabidaea patellifera* (Schltdl.) Sandwith (Bigoniaceae) in the ACG dry forest in the first month of the rainy season. The green and yellow larvae (Fig. 7) feed on the upper side of the nearly horizontal leaves. The early instars feed as a group, but, by the penultimate instars, they have separated to feed solitarily. The larvae drop to the ground to spin a very tough brown ovoid cocoon in the leaf litter. Between seven and 17 days lapsed between spinning and adult eclosion, but some larvae remained as dormant prepupae in their cocoons throughout the five remaining months of the rainy season and the entire six month dry season before dying, apparently because they did not get the right cue to eclose under laboratory conditions. This species has been found feeding on its common food plant only at the beginning of the rainy season, and it may well be univoltine in nature. No parasitoids were produced from 50 wild-caught larvae of all instars.

**Remarks.**—This species is very similar in coloration to *Acordulecera ricatus* (Konow) described from Peru, and both lack the seta on the apical antennal segment. However, *A. ricatus* has a hyaline forewing



Figs. 37–42. Tarsal claws and male genitalia, ventral view of left half of genital capsule on left, lateral view of penis valve on right. 37, Female tarsal claw of *Adiaclema chigiyac*. 38, Male tarsal claw of *A. chigiyac*. 39, Male genitalia of *A. chigiyac*. 40, Male genitalia of *Anathulea bimaculata*. 41, Male genitalia of *Acordulecera liami*. 42, Male genitalia of *A. dashielli*.

with the base and apex of the wings black, whereas *A. dashielli* has uniformly lightly blackish wings. The sheath is distinctive for *A. dashielli*, but other characters need to be compared with the illustrations for determination.

### ACKNOWLEDGMENTS

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## Review of the Southeastern Asian Sawfly Genus *Eusunoxa* Enslin (Hymenoptera: Tenthredinidae)

DAVID R. SMITH AND M. S. SAINI

(DRS) David R. Smith, Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0168, USA, email: dsmith@sel.barc.usda.gov;

(MSS) Department of Zoology, Punjabi University, Patiala, 147002 India  
email: saini20@glide.net.in

**Abstract.**—Nine species of *Eusunoxa* Enslin are keyed, described, and illustrated: *E. buchi* Togashi from the Philippines; *E. ceylonica* Malaise from Sri Lanka and southern India; *E. formosana* Enslin from Taiwan; *E. ebena*, n. sp., from Indonesia (Kalimantan); and *E. nigriceps* (Rohwer), *E. auri-cauda*, n. sp., *E. lissofrons*, n. sp., *E. punctata*, n. sp., and *E. semipunctata*, n. sp., from southern India. *Eusunoxa* subg. *Asunoxa* Wei is a new synonym of *Eusunoxa* Enslin, and *Eusunoxa indianica* Haris is a new synonym of *E. ceylonica* Malaise.

*Eusunoxa* Enslin, a small genus of the subfamily Allantinae, is known from India, Sri Lanka, Taiwan, Indonesia, and the Philippines. Malaise (1963) also mentioned Burma in the distribution of the genus, but we have not seen specimens from Burma, although one species was collected during extensive surveys of northeastern India by the junior author. Specimens are not common, but significant collections from southern India and Sri Lanka have prompted this review. We treat nine species, five of which are described as new. Food plants are not known.

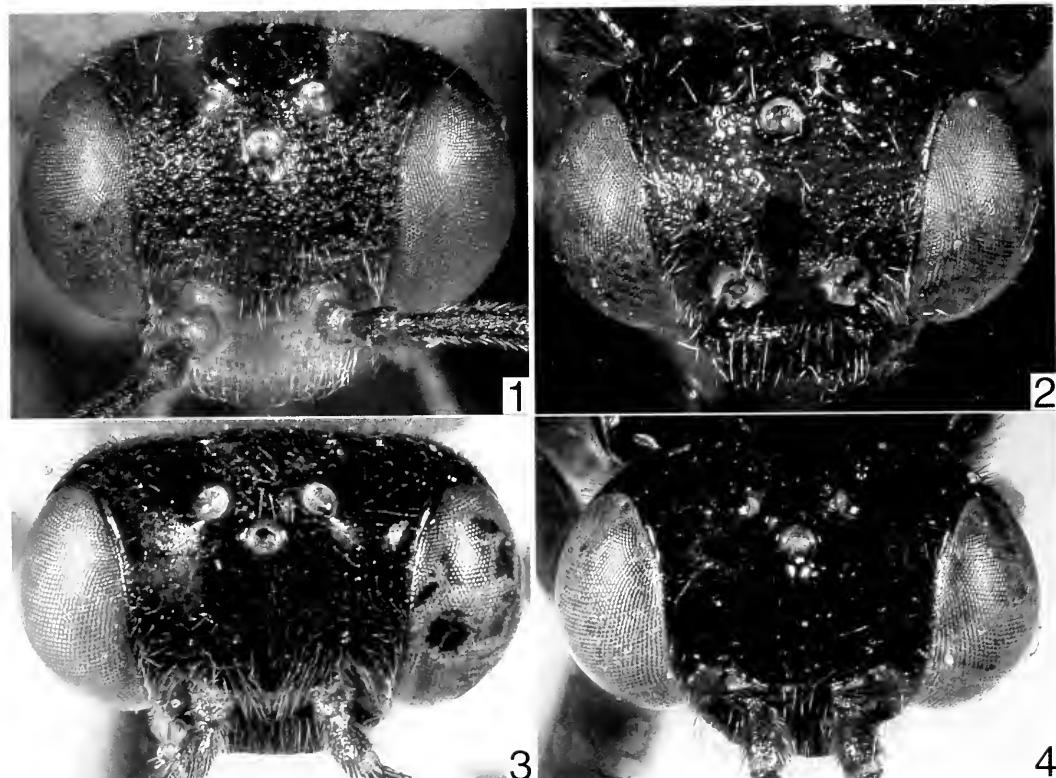
Acronyms used are: BMNH = The Natural History Museum, London, UK; DEI = Deutsches Entomologisches Institut, Eberswalde, Germany; PUNJ = Punjabi University, Patiala, India; USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. Abbreviations used are: OOL = distance between eye and hind ocellus; POL = distance between hind ocelli; OCL = distance between hind ocellus and posterior margin of head.

### *Eusunoxa* Enslin

*Eusunoxa* Enslin 1911: 99. Type species: *Eusunoxa formosana* Enslin, by original designation.

*Eusunoxa* subg. *Asunoxa* Wei 1997: 88. Type species: *Eusunoxa ceylonica* Malaise, by original designation. New synonymy.

**Description.**—Antenna filiform, sometimes slightly incrassate in middle and flagellomeres slightly serrate, length 2× or less head width; 1st and 2nd segments each longer than broad; 3rd segment subequal to or slightly longer than 4th; apical segments without ventral membranous areas. Head from above strongly narrowing behind eyes; postgenal carina absent; inner margins of eyes slightly converging downwards; clypeus subtruncate to very shallowly circularly emarginate (Fig. 2); labrum short, about 2× broader than long; malar space linear or very narrow to slightly more than half diameter of front ocellus. Head with frontal area about same height as eyes; supraantennal tubercles and frontal ridges indistinct; median fovea a shallow groove; supraantennal pits distinct, about 2× their di-



Figs. 1–4. Front view of head. 1, *Eusunoxa punctata*. 2, *E. semipunctata*. 3, *Eusunoxa ceylonica*. 4, *E. lissofrons*.

ameter from antennal socket and each with a small conical projection at center; lateral furrows deep and slightly diverging posteriorly; post-, inter-, and circumocellar furrows indistinct to absent. Epicnemium present as a flat sclerite separated from mesepisternum by a suture. Hind coxae lengthened, end of hind basitarsus reaching to and beyond apex of abdomen; hind basitarsus (Figs. 5–8) longer than length of remaining tarsal segments combined, broad and laterally flattened, with outer surface concave; tarsal pulvilli present only on segments 3 and 4. Tarsal claws with single inner tooth, slightly shorter than outer tooth, and positioned lateral to outer tooth; basal lobe present or absent. Hind wing with cell  $Rs$  absent, cell  $M$  present. Thorax and abdomen impunctate, shining.

*Discussion.*—The presence of an epicne-

mium, long hind legs with the hind basitarsus reaching to or beyond the apex of the abdomen, the large, laterally compressed hind basitarsus, and presence of one closed cell in the hind wing are distinctive for *Eusunoxa*. *Eusunoxa* may be separated from other Allantinae by Malaise's (1963) key. It is closest to *Megabeleses* Takeuchi, *Beleses* Cameron, and *Nesotaxonus* Rohwer, but *Megabeleses* has the inner tooth of the tarsal claws much longer than the apical one, much longer antennae (more than twice the head width), and the head from above slightly dilated behind the eyes. The other genera have a normal (cylindrical) hind basitarsus and have ventral membranous areas in the apical four antennal segments. The broad, laterally compressed hind basitarsus is reminiscent of the same in the Holarctic genus *Craesus* Leach (Nematinae).

Wei (1997) proposed the subgenus *Asunoxa* for those species lacking a basal lobe to the tarsal claws (Fig. 22). This included all known species except *E. formosana* Enslin, which has a basal lobe (Fig. 21) and was the only described species in the typical subgenus (Wei [1997] separated some unnamed species, designated as "E. spp." and we add one, *E. ebena*, n. sp., here).

Other than the basal lobe, *E. formosana* shares all other characters with other species, including similarities in the genitalia, and shares the presence of punctures on the frons with some other species. Because the presence or absence of a basal lobe is of suspicious importance, we do not see the necessity of recognizing subgenera at present.

#### KEY TO SPECIES OF *EUSUNOXA*

- 1 Tarsal claws with basal lobe (Fig. 21); front of head with large, closely set punctures separated by narrow ridges, as in Fig. 1 ..... 2
- Tarsal claws without basal lobe (Fig. 22); punctures on front of head as above, widely spaced with broad, flat, shining interspaces (Fig. 2) or absent (Figs. 3, 4) ..... 3
- 2 Head, thorax, and abdomen orange yellow; antenna black with basal segments orange; wings yellow hyaline, costa and subcosta yellowish, stigma brownish with margins yellowish; hind basitarsus 4.8× longer than maximum width (lancet in Fig. 9; male genitalia in Figs. 13, 14) ..... *formosana* Enslin
- Head (except for reddish-brown clypeus), thorax and abdomen black; wings lightly blackish with costa, subcosta and stigma black; hind basitarsus 3.8× longer than maximum width ..... *ebena*, n. sp.
- 3 Thorax black or black with pronotum, tegula, and part of meso- and metanotum dark orange ..... 4
- Thorax entirely orange ..... 7
- 4 Pronotum, tegula, V-shaped mark on mesoprescutum, mesoscutellum, and metanotum orange (head shining, impunctate, as in Fig. 4; male genitalia with penis valve curved, in Fig. 20) ..... *nigriceps* (Rohwer) (♂)
- Thorax entirely black ..... 5
- 5 Abdomen orange except for blackish basal plates (frons sparsely punctured, with shining interspaces, as in Fig. 2; male genitalia in Fig. 17) ..... *auricunda*, n. sp.
- Abdomen black ..... 6
- 6 Legs entirely black; head shining, impunctate (Fig. 4); penis valve oval (Fig. 19) ..... *lissofrons*, n. sp.
- Legs with fore- and midtibiae and tarsi white; head with sparse, widely separated punctures with shining interspaces on frons (Fig. 2); penis valve elongate, constricted at center (Fig. 18) ..... *semipunctata*, n. sp. (♂)
- 7 Clypeus and supraclypeal area dark orange; first antennal segment or basal 2 antennal segments and base of 3rd segment may be orange; head with frons densely punctate, punctures close together, separated by narrow ridges, without shining interspaces (Fig. 1) ..... 8
- Head and antenna black; frons impunctate, shining, or with widely spaced punctures separated by broad, shining interspaces (Figs. 2–4) ..... 9
- 8 Hind femur basally orange, apical half or more black; basal 2 antennal segments and base of 3rd segment orange; hind basitarsus about 1.4× length of remaining tarsal segments combined; Philippines ..... *buchi* Togashi
- Hind femur entirely black; only 1st antennal segment dark orange; hind basitarsus about

1.7× length of remaining tarsal segments combined (Fig. 8) (lancet in Fig. 11); India  
..... *punctata*, n. sp.

9 Femora blackish, only extreme bases may be orange; frons with distinct, widely spaced  
punctures, separated by broad, shiny interspaces (Fig. 2) (lancet in Fig. 12) ..... *semipunctata*, n. sp. (♀)

— Fore- and midfemora orange, hind femur entirely or partly black; frons with few minute  
punctures or impunctate, shining (Figs. 3, 4) ..... 10

10 Most of hind femur black, only extreme base orange; extreme apices of fore- and midtibiae  
black (lancet in Fig. 10; male genitalia in Figs. 15, 16) ..... *ceylonica* Malaise

— Apical half of hind femur black; tibiae orange (after Rohwer 1915) ..... *nigriceps* (Rohwer) (♀)

*Eusunoxa auricauda* Smith and Saini,  
new species  
(Fig. 17)

*Female*.—Unknown.

*Male*.—Length, 6.5 mm. Antenna, head, and thorax black, abdomen orange with black basal plates, basal plates darkest black laterally. Legs with apices of coxae and trochanters on upper surfaces white; fore- and midlegs with apices of femora and tibiae and tarsi entirely white; hind tibia black with white streak on inner surface of basal half. Wings lightly infumated towards apex; stigma, costa, and rest of venation dark brown to black. Antenna slightly compressed and flagellomeres serrate on underside with blunt projections on segments at apex below; length 2× head width; pedicel 2× its apical width; scape as long as its apical width; segment 3 slightly longer than segment 4. Clypeus with shallow V-shaped emargination; lower interocular distance 0.8× eye length; OOL:POL:OCL = 1.00:0.92:0.80; postocellar area subconvex, 3× broader than long at its maximum width; head with sparse, shallow punctures with flat shining interspaces on and around the frontal area (similar to Fig. 2), posterior orbits and postocellar area impunctate. Hind basitarsus 1.3× length of remaining tarsal segments combined, about 4.0× longer than maximum width. Tarsal claws without basal lobe. Genital capsule similar to Fig. 15; penis valve in Fig. 17.

*Holotype*.—♂, India, Kerala: Munar,

4000 ft., 22.9.1995, collection M.S. Saini  
(PUNJ).

*Distribution*.—India (Kerala).

*Etymology*.—The species name is based on the orange abdomen.

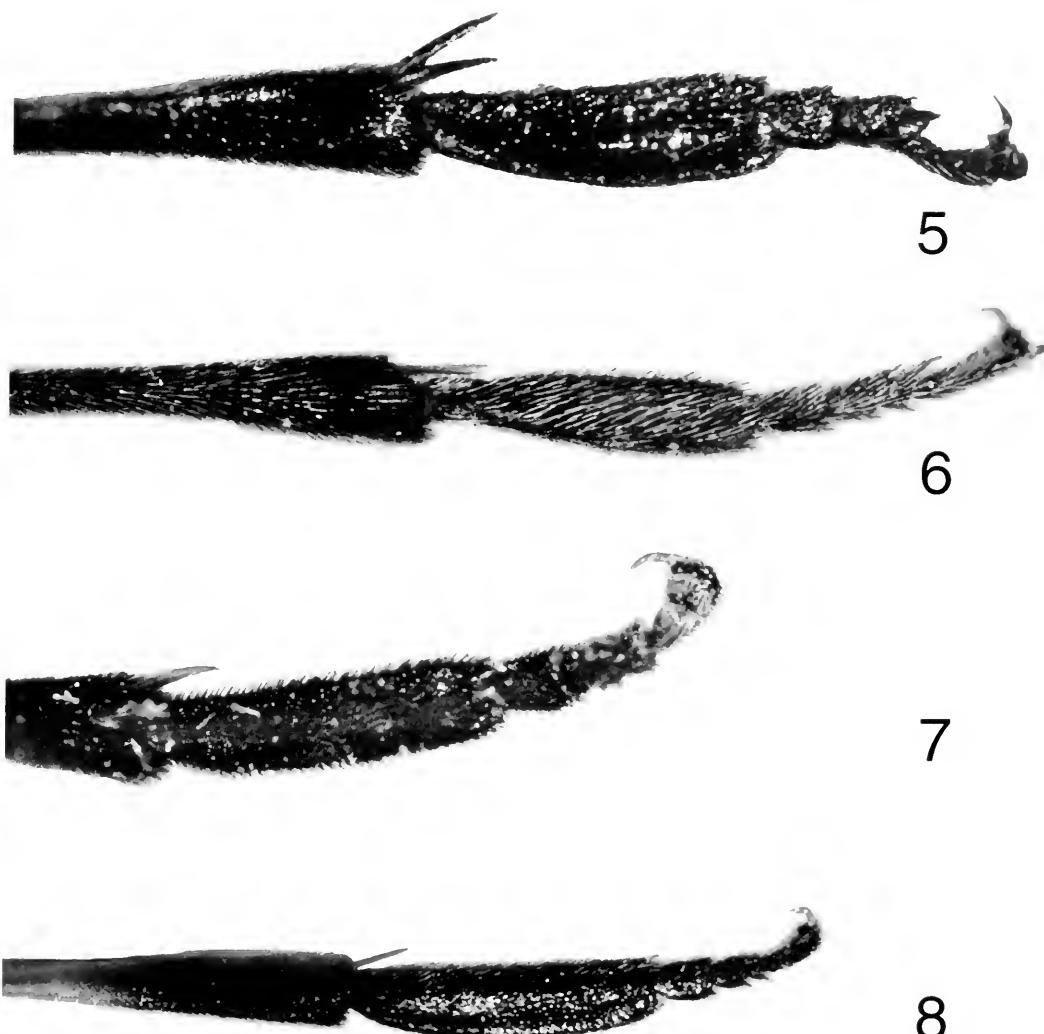
*Remarks*.—The black head and thorax with the contrasting orange abdomen are unlike other species of *Eusunoxa*. This coloration and the sparsely punctured head (similar to Fig. 2) will distinguish this species from other species in the genus. *Eusunoxa auricauda* is most similar to the male of *E. semipunctata*, with which it shares the punctate head, similar hind basitarsus, and very similar male genitalia (Figs. 17, 18). However, the absence of color variation in the large series of males of *E. semipunctata* and the slight difference in shape of the penis valve (less constricted at its center than that of *E. semipunctata*), provide evidence that *E. auricauda* is a separate species.

*Eusunoxa buchi* Togashi

*Eusunoxa buchi* Togashi 1981: 419, figs. 21–24, 26–28.—Wei 1997: 89 (in subg. *Asunoxa*; in key).

*Female*.—Unknown.

*Male*.—Length, 6.0 mm. Antenna black with segments 1, 2, and basal half of 3rd segment orange. Head black with clypeus, mouthparts, and supraclypeal area orange. Thorax and abdomen orange. Fore- and midlegs orange with apical 4 tarsal segments infuscate; hind leg with coxa and trochanter orange, femur black except



Figs. 5–8. Apex of hind tibia and hind tarsus. 5, *Eusunoxa ceylonica*. 6, *E. lissofrons*. 7, *E. semipunctata*. 8, *E. punctata*.

basal quarter orange, tibia black with basal third white, and tarsus black. Wings very lightly, uniformly infuscated; veins and stigma black. Antennal length  $1.7 \times$  head width; 3rd segment subequal in length to 4th. Lower interocular distance  $0.7 \times$  eye length. Postocellar area  $2.5 \times$  broader than long; clypeus subtruncate; malar space linear; OOL:POL:OCL = 1.00:0.80:0.80. Front of head densely punctate, punctures large and close together, separated by narrow ridges (similar to Fig. 1); postocellar and postocular areas nearly

impunctate, shining. Hind basitarsus  $1.4 \times$  length of remaining tarsal segments combined,  $4.2 \times$  longer than maximum width. Tarsal claws without basal lobe.

*Types*.—Holotype ♂, "Sept. 7, 1961, Mantalingajan, Pinigisan, 600 m, Palawan Is., Noona Dan Expedition," in Universitets Zoologiske Museum, Copenhagen, Denmark. Ten paratype males, dated Sept. 6–24, 1961, also in type series. None examined.

*Specimen examined*.—PHILIPPINES: Palawan, Mantalingajan, Pinigisan, 600 m, 23

Sept. 1961, Noona Dan Exp. 61-62 (1 ♂, BMNH). From same locality as type series.

*Distribution.*—Philippines (Palawan).

*Remarks.*—*Eusunoxa buchi* is the only species in the genus known from the Philippines. It shares the densely punctate head with *E. formosana*, *E. ebena*, and *E. punctata*. The mostly black coloration and lack of a basal lobe on the tarsal claws separate it from *E. formosana* and *E. ebena*, and the dark orange basal antennal segments and only the apical half of the hind femur black separate it from *E. punctata* from India, which has the hind femur black and only the first antennal segment dark orange.

***Eusunoxa ceylonica* Malaise**

(Figs. 3, 5, 10, 15, 16, 22)

*Netrocerus nigriceps* Enderlein 1920: 371. Preoccupied in *Eusunoxa* by *Eusunoxa nigriceps* (Rohwer 1915).

*Eusunoxa ceylonica* Malaise 1932: 147.—Smith 1982: 120, figs. 2, 8, 14 (Sri Lankan records; female lancet, male genitalia, tarsal claw figured; syn.: *N. nigriceps* Enderlein).—Saini and Deep 1994: 50 (India, Tamil Nadu; as “*ceylonica*”).—Wei 1997: 89 (in subg. *Asunoxa*; in key).

*Eusunoxa indiana* Haris 2000: 299. New synonymy.

*Female.*—Length, 6.5–7.5 mm. Antenna and head black; clypeus black to partially orange on side or anterior margins. Thorax and abdomen orange. Foreleg orange with extreme apex of tibia and apical 4 tarsal segments blackish; midleg orange with apical half of tibia and entire tarsus black; hind leg with coxa, trochanters, and basal third of femur orange, apical two-thirds of femur and entire tibia and tarsus black. Wings uniformly infuscated; veins and stigma black. Antennal length 1.7× head width, 3rd segment slightly longer than 4th. Lower interocular distance subequal to eye length; clypeus subtruncate; postocellar area 4.5× broader than long; malar space nearly linear; OOL:POL:OCL = 1.00:0.90:0.35. Head shining, impunctate

except for small widely scattered punctures on frontal area (Fig. 3). Hind basitarsus (Fig. 5) 1.5× length of remaining tarsal segments combined; about 3.6× longer than maximum width. Tarsal claws without basal lobe. Lancet in Fig. 10, with about 17 serrulae; apex roundly acute.

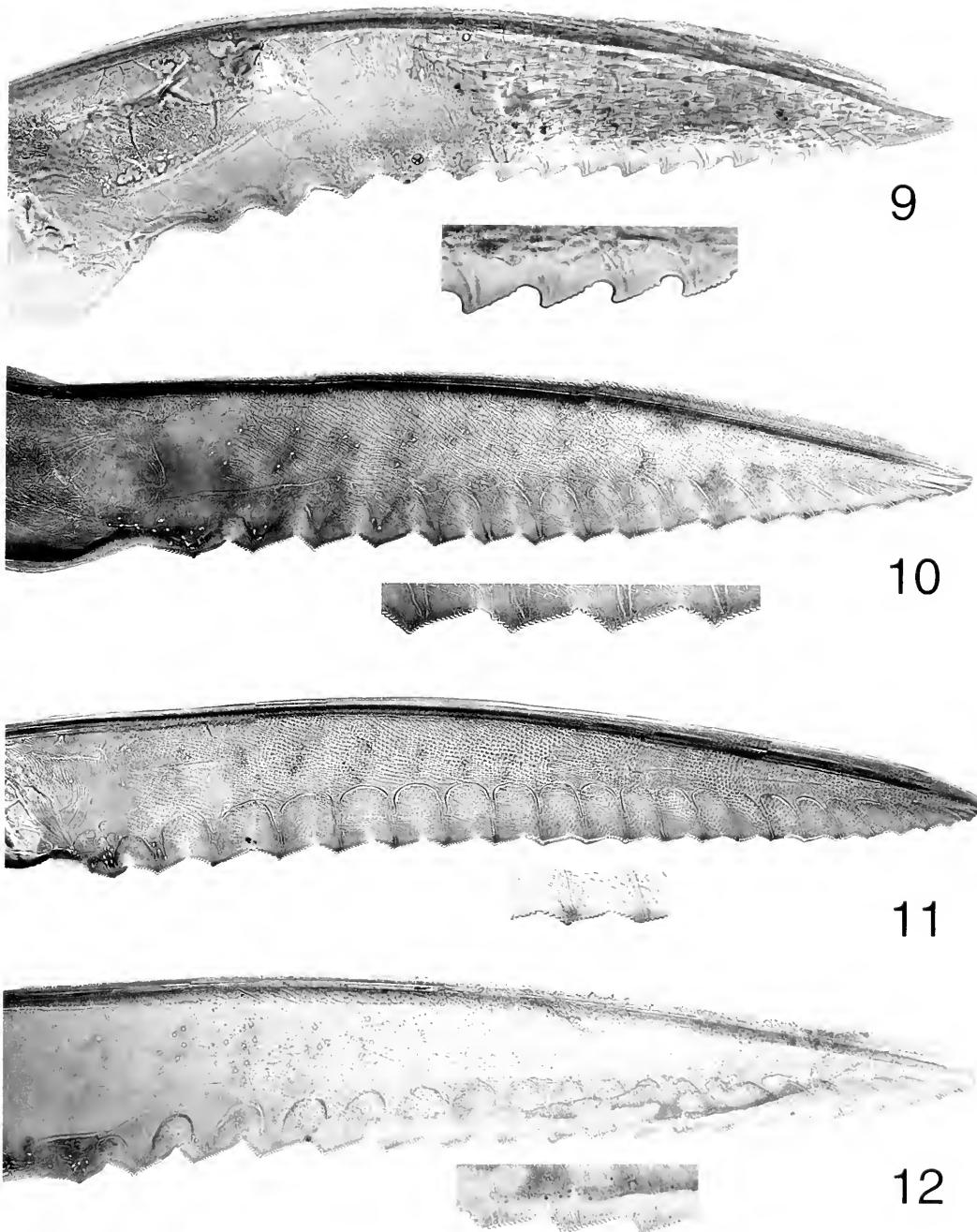
*Male.*—Length, 5.5–6.0 mm. Similar to female but with terga 2 to apex mostly infuscate to blackish and clypeus black or partly to almost entirely orange. Genitalia in Figs. 15, 16.

*Types.*—The holotype ♀ of *Netrocerus nigriceps* Enderlein, is in the Polish Academy of Sciences, Warsaw (examined). The holotype ♀ of *E. ceylonica* Malaise is in the BMNH, labeled “Colombo, Ceylon”; a paratype from the Swedish Museum of Natural History was examined. The holotype of *E. indiana* Haris is at the BMNH (examined), a ♂ labeled: “Holotype,” “India, Tamil N., Madras, 2.XI.79. Boucek,” “Holotype *Eusunoxa indiana* sp. n. det. A. Haris 1999,” “B.M. type Hym. 1.851.”

*Specimens examined.*—INDIA: Poonmudi, 18-9-95 (1 ♀); South India, Anamalai Hills, Cinchona, 3500 ft., V-1964, P.S. Nathan (2 ♀), V-1966 (2 ♀), X-1966 (1 ♀), V-1967 (1 ♀), V-1968 (1 ♀); Nilgiri Hills, Singara, S. India, 3400 ft., June 1954, col: P.S. Nathan (1 ♀); South India, Kerala State, Trivandrum Dt., Poonmudi Range, May 1971, 3000 ft. elevation, T.R.S. Nathan (2 ♀); South India, Pondicherry State, Karikal, P.S. Nathan (1 ♀), same but with date, X-62 (1 ♀). SRI LANKA: Western Province, Central Province, Southern Province, Eastern Province, North Western Province, Northern Province (see Smith 1982 for records); Ceylon, Trincomalee (1 ♀, BMNH).

*Distribution.*—India (Kerala; Tamil Nadu); Sri Lanka.

*Remarks.*—*Eusunoxa indiana* Haris is the male of *E. ceylonica*. It is typical except for the orange clypeus. We have not seen other specimens with an entirely orange clypeus; however, among the material we examined, coloration varies from black to



Figs. 9–12. Female lancets. 9, *Eusunoa formosana*. 10, *E. ceylonica*. 11, *E. punctata*. 12, *E. semipunctata*.

brownish, to some partially orange at the base and laterally.

The specimen from Ceylon at BMNH is like *E. ceylonica*, but the head (off the spec-

imen and glued on cardboard on the same pin) is more punctate than most specimens.

We have not seen variation in color of

the thorax and abdomen, both are mostly orange, with the abdomen of the male more blackish dorsally. *Eusunoxa ceylonica* appears to be most similar to *E. nigriceps*, both sharing the shining head with few widely spaced punctures, and the female is difficult to distinguish from that of *E. nigriceps* based on Rohwer's (1915) description of the latter. The male paratype of *E. nigriceps*, however, is mostly black, and the genitalia differ (Figs. 16, 20) from that of *E. ceylonica*.

In Sri Lanka, this species occurs in both open and wooded areas in dry and wet zones with annual rainfall ranging from 660 to 1952 mm (Smith 1982).

*Eusunoxa ebena* Smith and Saini,  
new species

**Female.**—Length, 8.0 mm. Antenna black with segments 1, 2, and basal half of 3 dark orange; head black with clypeus reddish brown. Thorax and abdomen black. Foreleg dark brown with coxa and apical 3 tarsal segments black; midleg with coxa black, femur and tibia dark brown (tarsus missing); hind leg black with basal half of tibia white (apical two tarsal segments missing). Wings very lightly, uniformly infuscated; veins and stigma black. Antennal length  $1.6 \times$  head width, 3rd segment  $1.1 \times$  longer than 4th. Lower interocular distance  $0.8 \times$  eye length; clypeus very shallowly circularly emarginated; postocellar area  $2.7 \times$  broader than long; malar space distinct, slightly more than half diameter of front ocellus; OOL:POL:OCL = 1.0:1.2:1.0. Head with frontal area densely punctured, punctures deep, close together, separated by narrow ridges (similar to Fig. 1); clypeus impunctate, shining; postocellar area and head behind eyes sparsely punctate, shining. Hind basitarsus extremely flat and concave;  $3.8 \times$  longer than maximum width (length to remaining tarsal segments unknown since apical tarsal segments missing). Tarsal claws with basal lobe (Fig. 21).

**Male.**—Unknown.

**Holotype.**—♀, "Borneo, Pontianak, F. Muir" (BMNH).

**Distribution.**—In present-day Kalimantan, Indonesia.

**Etymology.**—The name is based on the almost entirely black coloration of this species.

**Remarks.**—*Eusunoxa ebena* and *E. formosana* are the only species that have a basal lobe on the tarsal claws. Also, both share the densely punctate frons. The coloration of the two are, however, entirely different. *Eusunoxa ebena* is almost entirely black and *E. formosana* almost entirely orange yellow. The hindbasitarsus is extremely flat, thin, and concave on its outer surface, similar to that of *E. formosana*. Because of the fragility of the specimen, the lancet was not examined; however, from the small apical part visible the serrulae appear to be rather deep similar to *E. formosana* (Fig. 9).

*Eusunoxa formosana* Enslin  
(Figs. 9, 13, 14, 21)

*Eusunoxa formosana* Enslin 1911: 99.—Wei 1997: 88 (in subg. *Eusunoxa*; in key).

**Female.**—Length, 7.5–8.0 mm. Antenna, head, thorax, and abdomen yellowish orange, with antennal segments 5–9, apical third to half of hind femur, and most of hind tarsus black; apical segments of hind tarsus paler, more dark orange. Wings yellow hyaline, costa and subcosta yellowish, stigma brownish with margins yellowish, rest of venation dark brown. Antenna filiform, very slightly incrassate in middle; antennal length  $1.7 \times$  head width; 3rd segment  $1.1 \times$  length of 4th; pedicel as long as its apical width; scape slightly longer than its apical width. Clypeus subtruncate; malar space distinct but much less than half diameter of front ocellus; lower interocular distance  $0.8 \times$  eye length. OOL:POL:OCL = 1.00:1.00:0.83, postocellar area convex,  $2 \times$  broader than long at its maximum breadth. Head with frons densely punctured, punctures deep,

close together, separated by narrow ridges (similar to Fig. 1); postocellar area and head behind eyes sparsely punctate, shining. Tarsal claws with inner tooth shorter than apical one, basal lobe distinct (Fig. 21). Hind basitarsus extremely flat and concave on its outer surface,  $1.7 \times$  length of remaining tarsal segments combined;  $4.8 \times$  longer than maximum width. Lancet in Fig. 9, serrulae deep with almost perpendicular anterior margin.

**Male.**—Length, 7.5 mm. Similar in color and structure to female. Genitalia in Figs. 13, 14.

**Type.**—Described from a female from "Formosa," in the Zoologisches Staats-sammlung, München, Germany; not examined.

**Specimens examined.**—TAIWAN: Taihor-in, Formosa, H. Sauter, 7.VI.1911 (1 ♀, USNM); Kankau (Koshun) Formosa, H. Sauter, VI-1912 (1 ♀, USNM), same except VII-1912 (1 ♀, DEI); PingTung Co., Kent-ing Bot. Garden, subtropical forest, July 10-14, 1980, 260 m, D.R. Davis (1 ♂, USNM); Formosa, Sauter, Taihorinaho, 1090.VIII (1 ♀, BMNH).

**Distribution.**—Taiwan.

**Remarks.**—We did not examine the type since the description and uniqueness of this species is sufficient for its identity. This and *E. ebena* are the only species of *Eusunoxa* with a basal lobe on the tarsal claws and one of the few species (other than *E. ebena*, *E. punctata* and *E. buchi*) with a densely punctate frons. The almost entirely orange coloration is also distinctive. The female ovipositor, especially the shape of the serrulae (Fig. 9), differs from other species of *Eusunoxa*. Male genitalia (Figs. 13, 14) differ from other species by the longer parapenis of the genital capsule.

***Eusunoxa lissofrons* Smith and Saini,  
new species  
(Figs. 4, 6, 19)**

**Female.**—Unknown.

**Male.**—Length, 5.5-6.0 mm. Head and

thorax black, abdomen and fore- and mid-legs brownish, hind leg black. Wings infumated apically from base of stigma, basal half clear; venation dark brown to black. Antennal length  $1.7 \times$  head width, slightly compressed and only feebly incrassate in middle; pedicel  $2 \times$  longer than its apical width; scape as long as broad at apex; 3rd segment  $1.1 \times$  longer than 4th. Clypeus subtruncate; lower interocular distance  $0.9 \times$  eye length; malar space distinct but much less than half diameter of front ocellus; OOL:OCL:POL = 1.00:1.00:0.70; postocellar area convex,  $2.8 \times$  broader than long. Head (Fig. 4), thorax, and abdomen smooth, impunctate, with polished surface. Hind basitarsus about  $1.2 \times$  length of remaining tarsal segments combined, about  $4.0 \times$  longer than maximum width. Tarsal claws without basal lobe. Genital capsule similar to Fig. 15, penis valve in Fig. 19.

**Holotype.**—♂, "South India, Anamalia [Anamalai ?] Hills, Cinchona, 3500 ft., V-1965, P.S. Nathan" (USNM).

**Paratypes.**—INDIA: Same data as holotype (1 ♂, USNM), same except V-1964 (1 ♂, USNM), X-1967 (2 ♂, USNM); Coimbatore, S. India, 9.7.1949, P. Susai Nathan (1 ♂, USNM); Kerala: Permade, Parryar, 3500 ft., 21-9-1995, coll. M.S. Saini (1 ♂, PUNJ).

**Distribution.**—India (Kerala, Tamil Nadu).

**Etymology.**—The species name is based on the shining, impunctate frons.

**Remarks.**—The impunctate, shining frons is similar to that of *E. ceylonica* and *E. nigriceps*, but the entirely black coloration precludes the association of *E. lissofrons* because color variation has not been observed in males of those species. The male of *E. nigriceps* has the thorax partly orange, and the male of *E. ceylonica* has the thorax and abdomen mostly orange, unlike the entirely black thorax and abdomen of *E. lissofrons*. The male penis valve of *E. lissofrons* (Fig. 19) is oval and similar to that of *E. ceylonica* (Fig. 16); it is less

similar to the curved valve of *E. nigriceps* (Fig. 20). There is no indication that *E. lissofrons* is a color variant, but, if so, it could be one of *E. ceylonica*.

***Eusunoxa nigriceps* (Rohwer)**  
(Fig. 20)

*Beleses nigriceps* Rohwer 1915: 51.

*Eusunoxa nigriceps*: Smith 1982: 120.—Wei 1997: 89 (in subg. *Asunoxa*; in key).

**Female.**—From Rohwer (1915). “Length, 6 mm.” “Head and posterior femora beyond middle, four posterior tarsi and the antennae black, the rest of the insect rufous.” “Wings distinctly hyaline, venation dark brown.” “Clypeus truncate, surface coarsely, irregularly punctured;” “front and posterior orbits shining, impunctate;” “flagellum gradually thickened until it reaches the apex of the second joint;” “the fourth and following joints compressed; thorax shining, impunctate.”

**Male (paratype).**—Length, 6.2 mm. Antenna and head black. Thorax blackish with tegula, pronotum, V-shaped mark on mesoprescutum, mesoscutellum, and metanotum dark orange. Abdomen mostly black. Foreleg orange with tarsus black; midleg with coxa, trochanter, and femur orange, tibia and tarsus black; hind leg with coxa, trochanter, and basal third of femur orange, apical two-thirds of femur and entire tibia and tarsus black. Wings lightly, uniformly infuscated; veins and stigma black. Antennal length  $1.7 \times$  head width; 3rd segment about  $1.1 \times$  length of 4th. Lower interocular distance  $0.8 \times$  eye length; postocellar area  $2.6 \times$  broader than long; clypeus subtruncate; malar space linear; OOL:POL:OCL = 1.00:1.00:0.74. Head shining, impunctate with very few punctures between antennae and eyes (similar to Fig. 4). Hind basitarsus  $1.5 \times$  length of remaining tarsal segments combined, about  $2.5 \times$  longer than maximum width. Tarsal claws without basal lobe. Genital capsule similar to Fig. 15; penis valve in Fig. 20, markedly curved in lateral view.

**Types.**—“Described from one female from Marikuppam, . . . 3,500 feet” and from “two males, one allotype, from Bangalore, . . . 3,000 feet” (South India). Type and allotype in the Indian Museum, as stated by Rohwer (1915), but we could not locate them and they are apparently no longer in existence. One paratype male is in the USNM, labeled “Ind. Mus., Bangalore, S. India, ca. 3000 ft., 12-X-10, Annandale,” “U.S.N.M. Paratype No. 18909.”

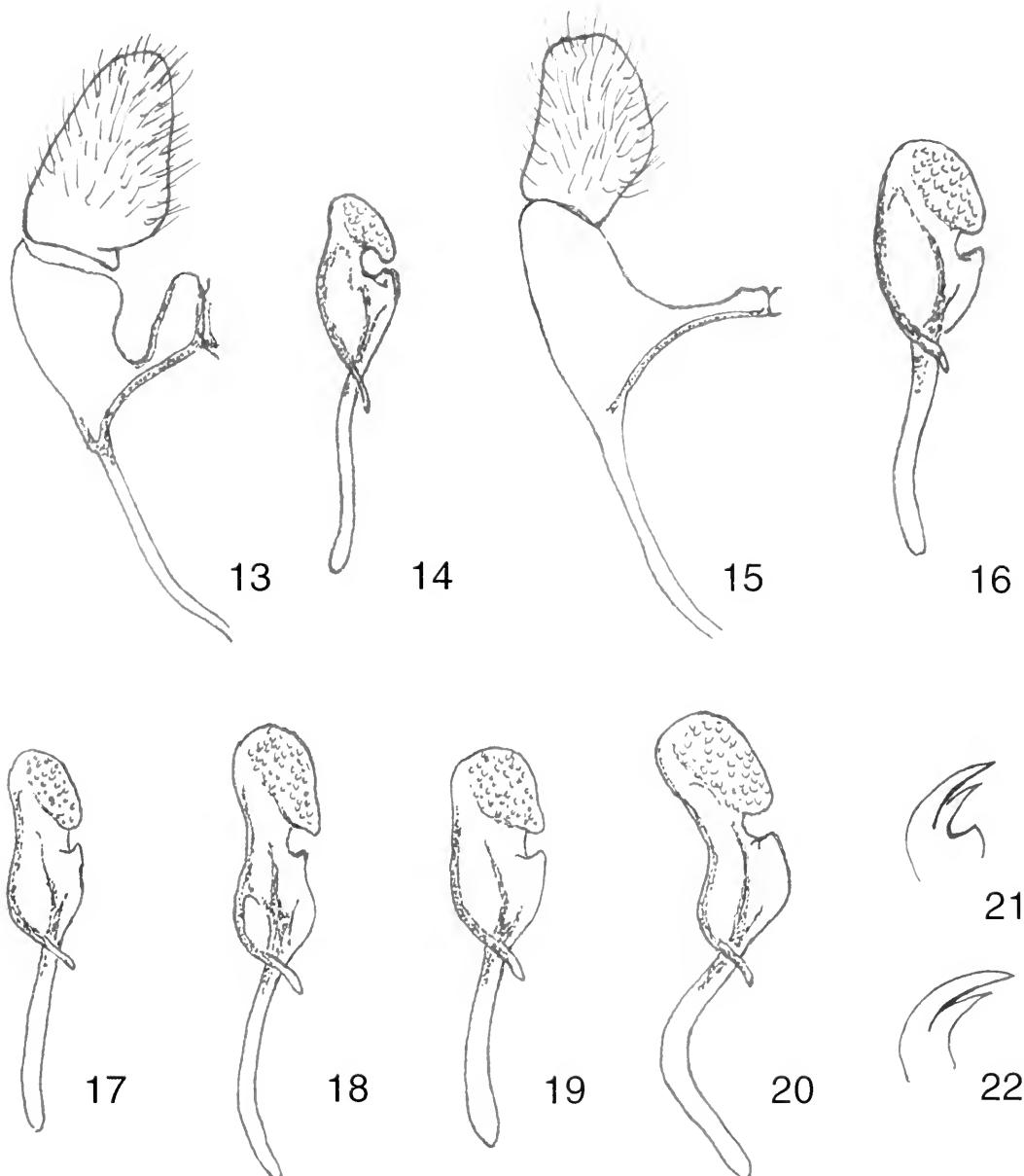
**Distribution.**—India (Karnataka).

**Remarks.**—Rohwer mentioned claws cleft, with the inner teeth exceeding the outer. Because the teeth are lateral and the paratype examined has the inner tooth shorter, Rohwer probably meant the outer tooth is longer.

Because we could not examine the holotype female, we assume Rohwer’s association of sexes was correct. The description of the female is based on Rohwer’s (1915) original description. It is very similar to the female of *E. ceylonica* and, so far as we can determine, can only be separated by the orange coloration of the tibiae and hind femur (see preceding key). Separation of *E. nigriceps* is based on the paratype male which, unlike most species and shared only by *E. lissofrons* and *E. ceylonica*, has the head shining and impunctate. However, the male of *E. lissofrons* is entirely black, and the male of *E. ceylonica* has the thorax and abdomen almost entirely orange. The shape of the male penis valve (Fig. 20) is markedly different from those species, and it is based on this feature that we believe *E. nigriceps* is a valid species and not a color variation of the others. We have not seen specimens that match Rohwer’s description of the female or the paratype male examined. Thus, we keep *E. nigriceps* a separate species until more material is available for evaluation of its status.

***Eusunoxa punctata* Smith and Saini,  
new species**  
(Figs. 1, 8, 11)

**Female.**—Length, 8.2 mm. Head and antenna black with 1st antennal segment,



Figs. 13–22. 13–20, Male genitalia. 13, Genital capsule, ventral view of left half, of *Eusunoxa formosana*. 14, Penis valve, lateral, of *E. formosana*. 15, Genital capsule, ventral view of left half, of *L. ceylonica*. 16, Penis valve of *E. ceylonica*. 17, Penis valve of *E. auricauda*. 18, Penis valve of *E. semipunctata*. 19, Penis valve of *E. lisoifrons*. 20, Penis valve of *E. nigriceps*. 21–22, Tarsal claws. 21, *E. formosana*. 22, *E. ceylonica*.

area below antenna, clypeus, labrum, mouthparts, mandible except tip, and very dim spots lateral to lateral furrows dark orange. Thorax and abdomen orange, except tergites 2–7 dark brownish at center.

Legs orange with midtarsus, apical two-thirds of hind femur, apical half of hind tibia, and entire hind tarsus black. Wings hyaline, infumated on apical half; stigma and costa brownish, rest of venation dark

brown to black. Antenna subincrassinated in middle, antennal length  $1.7 \times$  head width; pedicel  $2 \times$  its apical width; scape as long as its apical width; 3rd and 4th antennal segments subequal in length. Clypeus truncate; lower interocular distance subequal to eye length; malar space distinct but much less than half diameter of front ocellus; OOL:POL:OCL = 1.00:0.96:0.96; postocellar area subconvex,  $2.4 \times$  broader than long. Frons densely punctate, punctures large and close together, separated by narrow ridges (Fig. 1); hind orbits and postocellar area less punctured, shining. Hind basitarsus (Fig. 8)  $1.7 \times$  length of remaining tarsal segments combined;  $3.7 \times$  longer than its maximum width. Tarsal claws without basal lobe. Lancet as in Fig. 11, with about 21 serrulae.

*Male*.—Unknown.

*Holotype*.—♀, Nagaland: Chuchuyin-long, 2800 ft., 9.5.1994, collection M.S. Saini (PUNJ).

*Distribution*.—India (Nagaland).

*Etymology*.—The species name is based on the densely punctate frons.

*Remarks*.—In *E. punctata*, the hind basitarsus is unusually long in comparison to the length of the remaining tarsal segments, and the frons is densely punctate, both character states of which are shared only with *E. formosana* and *E. ebena*. *Eusunoxa formosana*, however, is almost entirely orange yellow and both *E. formosana* and *E. ebena* have a basal lobe on the tarsal claws. The shape of the serrulae of the lancets of *E. punctata* and *E. formosana* also differ (Fig. 9, 11). The only other species with a densely punctate frons and absence of a basal lobe on the tarsal claws is *E. buchi* from the Philippines. However, *E. buchi* has a shorter hind basitarsus, only about  $1.4 \times$  the length of the remaining tarsal segments combined, and the basal two and basal half of the third antennal segments are dark orange.

*Eusunoxa semipunctata*  
Smith and Saini, new species  
(Figs. 2, 7, 12, 18)

*Female*.—Length, 7.2–8.0 mm. Antenna and head black. Thorax and abdomen orange, upper half of mesepisternum somewhat more whitish than orange. Legs with coxae blackish except apices, trochanters white, femora blackish except extreme bases orange, fore- and midtibiae and fore- and midtarsi white with apical 3–4 tarsal segments infuscated to black. Wings lightly infumated apically from base of stigma, basal halves clear, venation dark brown to black. Antenna subincrassinated in middle, antennal length  $1.8 \times$  head width; pedicel and scape each  $2 \times$  longer than their apical widths; 3rd segment very slightly longer than 4th. Clypeus subtruncate; lower interocular distance subequal to eye length; malar space nearly linear; OOL:POL:OCL = 1.00:0.80:0.68; postocellar area subconvex,  $2.9 \times$  broader than long. Frons with distinct but sparse, widely separated punctures with broad, shiny interspaces between them (Fig. 2). Hind basitarsus (Fig. 7)  $1.3 \times$  length of remaining tarsal segments combined;  $3.9 \times$  longer than maximum width. Tarsal claws without basal lobe. Lancet as in Fig. 12, with about 20–21 serrulae.

*Male*.—Length, 6.5–7.0 mm. Antenna, head, and thorax black. Color of legs similar to that of female. Structure similar to that of female. Genital capsule similar to Fig. 15, penis valve in Fig. 18.

*Holotype*.—♀, “South India, Madras State. Anamalai Hills, Kadamparai, 3500', V-'63, P.S. Nathan” (USNM).

*Paratypes*.—INDIA: Same data as holotype (12 ♀, 43 ♂); Nilgiri Hills, Naduvattam, S. India, 6000 ft., May 1958, P.S. Nathan (1 ♂); South India, Anamalai Hills, Cinchona, 3500 ft., IV-1969, P.S. Nathan (6 ♂); V-1964 (4 ♂); V-1965 (4 ♀, 1 ♂); V-1966 (3 ♂); V-1967 (4 ♀, 2 ♂); IV-1969 (1 ♂); V-1968 (2 ♀, 2 ♂); V-1969 (2 ♀, 2 ♂); IX-1969, T.R.S. Nathan (1 ♂); Poomundi, 1550 m,

Kerala, India, 19-9-95 (1 ♂) (all USNM); Kerala: Poonmudi Hills, 4800 ft., 18.5.1995, collection M.S. Saini (1 ♂, PUNJ).

*Distribution.*—India (Kerala).

*Etymology.*—The name is based on the presence of widely spaced punctures on the frons.

*Remarks.*—Association of sexes is based on series taken at the same localities and at the same time. Only the coloration of the thorax and abdomen differs; the males black and the females orange. Such color dimorphism is not unusual in sawflies, and *E. nigriceps* apparently also shows color dimorphism. However, males of *E. ceylonica* and *E. formosana* are similar in color to the females. Both sexes of *E. semipunctata* have the distinct but widely spaced punctures on the frons with shining interspaces (as in Fig. 2). The female is separated from those of other species of *Eusunoxa* by the mostly black femora, and the male by the mostly black legs with the fore- and midtibiae and tarsi white. The punctuation of the head also separates the female; no other species with an orange thorax and abdomen have such dense punctures. The male is similar to *E. auricauda*, but the abdomen of *E. auricauda* is orange (see remarks under that species).

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## Larval Anatomy of Orussidae (Hymenoptera)

LARS VILHELMSEN

Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100, Denmark,  
e-mail: lbvilhelmsen@zmuc.ku.dk

**Abstract.**—The external and selected parts of the internal anatomy of the larva of *Orussus abietinus* (Orussidae) are examined. The external anatomy is similar to that reported for other Orussidae. The eyes, laterocervicalia, and thoracic legs are absent, and the antennae, maxillae, and labium are reduced. Each thoracic and abdominal segment has a pair of short transverse rows of recurved cuticular spines laterodorsally, probably for locomotory purposes. A previously unreported feature is the configuration of the hindgut, which has a set of transverse interlocking cuticular folds. The mid- and hindgut are anatomically continuous. Overall, the larval anatomy of Orussidae is highly reduced compared with that of other basal hymenopteran lineages and resembles that of apocritan larvae. The modifications of the larval anatomy are probably correlated with the shift in lifestyle from herbivorous to carnivorous, which is less demanding of the sensory, feeding, and locomotory apparatus.

Orussidae is a small wasp family, comprising 75 species worldwide (Vilhelmsen in press). Traditionally, the Hymenoptera have been subdivided in two suborders, the almost exclusively herbivorous 'Symphyta' and the predominantly entomophagous Apocrita; Orussidae were usually placed in the 'Symphyta' because of the absence of the wasp-waist in the adults, the defining feature of the Apocrita. However, recent phylogenetic treatments of the Hymenoptera unequivocally have retrieved Orussidae + Apocrita as an extremely well supported clade (Ronquist et al. 1999, Vilhelmsen 2001). Information on the biology of most species of Orussidae is scarce or non-existent; what evidence there is (see Vilhelmsen et al. 2001) indicates that the larvae are ectoparasitoids of woodboring insect larvae, usually Buprestidae (Coleoptera). This was probably the lifestyle of the common ancestor of all parasitoid Hymenoptera. The position of the woodboring 'siricoid' superfamilies as successive outgroups to the Orussidae-Apocrita clade indicates that the parasitoid lifestyle evolved via a woodboring in-

termediate in Hymenoptera (Hanson and Gauld 1995; Vilhelmsen 1997).

Nutall (1980) provided a very brief description of the larva of *Guiglia schauinslandi* (Ashmead, 1903), a New Zealand species. The only detailed descriptions of the immature stages of an orussid species are by Rohwer and Cushman (1917) and Parker (1935), who dealt with *Orussus occidentalis* Cresson, 1879, a Nearctic species. The section on Orussidae in Yuasa's (1922) treatment of non-apocritan larvae is based entirely on Cushman and Rohwer (1917). They noted that the larva of *Orussus* share many traits with those of apocritan Hymenoptera (eyes, most head appendages, and thoracic legs very reduced), whereas the anatomy of adult Orussidae apparently resembles that of 'Symphyta'. This mix of features and the parasitoid lifestyle led Rohwer and Cushman (1917) to erect a new suborder, the Idiogastra, comprising just the Orussidae.

Parker (1935) observed a few internal features of the head anatomy of *O. occidentalis*, but otherwise information about the internal larval anatomy of the family

is wanting. Orussidae were not included in the survey of 'symphytan' larvae by Maxwell (1955). Specifically, it is not known whether there is any connection between the mid- and hindgut. The separation of these gut sections and the postponement of voiding of the gut contents (as a meconium) until just prior to pupation is a near universal feature of the Apocrita (Hanson and Gauld 1995; Quicke 1997); it usually is interpreted as an important adaptation to the parasitoid lifestyle, especially endoparasitism, apparently serving to prevent contamination of the host. However, the condition in Orussidae and some of the putatively basal apocritan taxa (Stephanidae, Megalyridae) has not been investigated, making it impossible to deduce exactly when the feature arose in the evolutionary history of parasitic Hymenoptera.

In the present study, I investigate the larval anatomy of two species of Orussidae in some detail. In addition to the external features already described by Rohwer and Cushman (1917), selected internal features are examined. The findings are discussed in relation to features observed in other hymenopteran larvae.

#### MATERIALS AND METHODS

Larvae of *Orussus abietinus* (Scopoli, 1763) and *Guiglia schauinslandi* (Ashmead, 1903) were available for study. Unfortunately, only the material of the former was in good condition, having been collected recently (1998 or later) and preserved in 80% ethanol or Pampels fluid and subsequently transferred to ethanol. In total, five larvae of *O. abietinus* were examined. Of these, four were final instars or prepupae, collected in early spring prior to pupation, and one was an early instar collected later in spring on a moldy pupa of *Buprestis* sp. (Coleoptera, Buprestidae). Four larvae of *G. schauinslandi* were examined. All were in rather poor condition, having been preserved in 95% ethanol for 40+ years after having initially been col-

lected in a kerosene-acetic acid-dioxane solution (KAAD). Only a limited number of observations of the external anatomy could be carried out on these specimens.

*External features.*—Initial examination of external features on specimens kept in ethanol was carried out with a Leica MZ Apo dissection microscope.

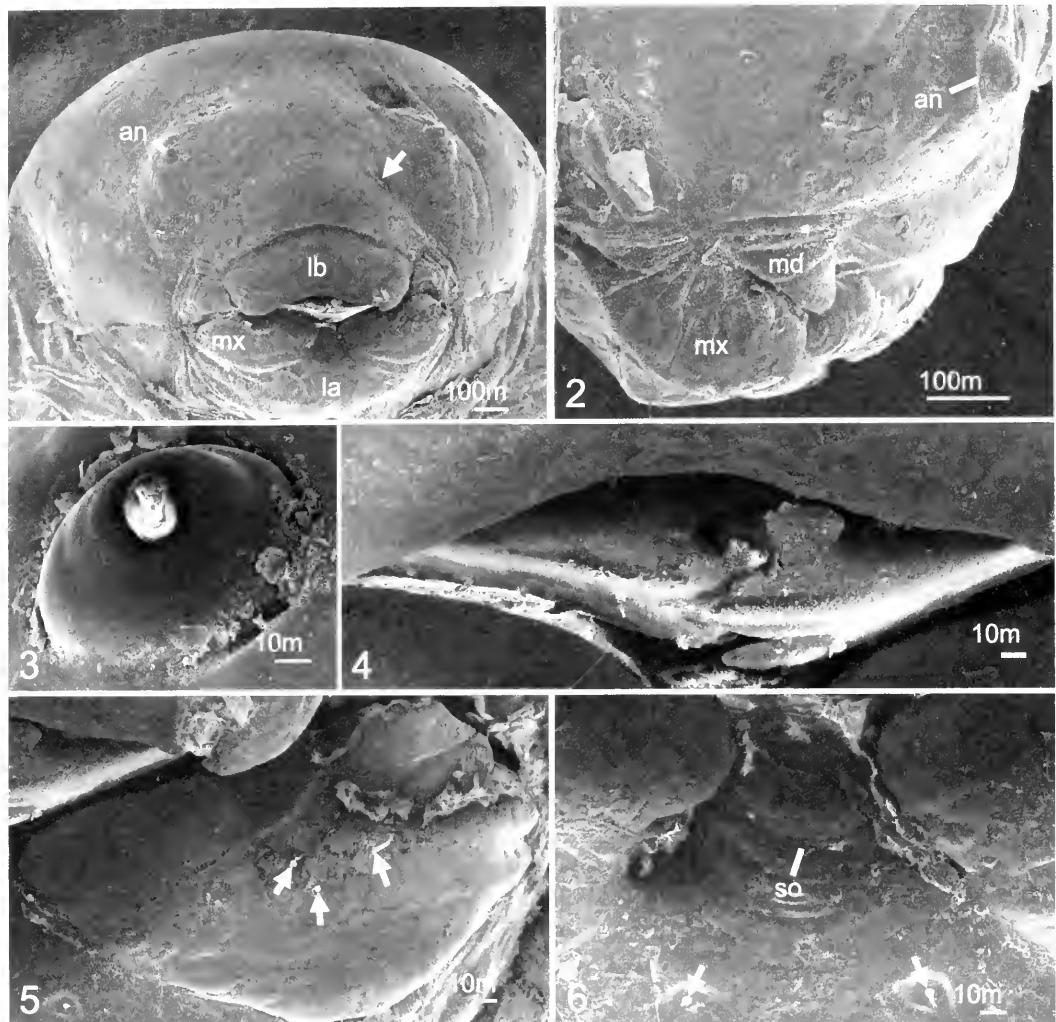
*SEM.*—Specimens preserved in ethanol were critically point dried and coated with Pt/Pd in a Jeol JFC-2300HR high resolution fine coater. They were examined with a Jeol JSM-6335F field emission scanning electron microscope.

*Histological sections.*—Specimens preserved in ethanol or Pampels fluid were dehydrated in butanol and embedded in paraplast. Sagittal sections of 8–12  $\mu\text{m}$  thickness, depending on the size of the specimen, were cut with a microtome. The sections were treated in a trichrome stain (Weigert's haematoxylin-bluish erythrosin-fast green, preceded by phosphomolybdic acid); permanent preparations were made in entellan.

#### RESULTS

The descriptions are based entirely on the prepupae and early instar of *O. abietinus*. The observations that could be made on the *G. schauinslandi* specimens did not reveal any significant differences between the two species.

*Overall.*—Body elongate, dorsoventrally flattened (less conspicuous in early instar). Body outline in cross-section with distinct bend laterally between upper and lower surface. Head hypognathous, boundary between head and prothorax indistinct in early instar, especially laterally. Segment boundaries otherwise distinctly demarcated by deep furrows dorsally, especially on abdomen. Body cuticle wrinkled, but without regular transverse annuli or other regular intrasegmental subdivisions. Small trichoid sensilla scattered over body surface. All thoracic and abdominal segments dorsally with paired, transverse rows of 2–4 (early instar) or 3–5 (prepupa)



Figs. 1–6. *Orussus abietinus*, head anatomy. 1, 3–6. Prepupa. 1, Head, ventral view, arrow indicates position of anterior tentorial pit: an = antenna; la = labium; lb = labrum; mx = maxilla. 2, Early instar larva, mouthparts, lateral view: md = mandible (only base visible). 3, Antenna. 4, Tips of mandibles, ventral view. 5, Maxilla, arrows indicate trichoid sensilla (two leftmost broken). 6, Labium, arrows indicate trichoid sensilla; so = salivary orifice.

slightly recurved cuticular spines submedially (Figs. 7–10).

**Head.**—Head capsule weakly sclerotized. Eye absent. Antenna one-segmented, short, rounded, situated lateroventrally on head capsule (Figs 1–2), distally with two short peglike sensilla in shallow depression (Fig. 3). Clypeus weakly delimited dorsally; anterior tentorial pits faintly visible as shallow, elongate depressions

(Fig. 1). Circular cuticular structure present medially of anterior tentorial pits, not visible externally. Small, transversely elongate sclerite present between clypeus and labrum. Labrum fleshy, slightly bifid apically, with 7–8 trichoid sensilla antero-laterally. Mandibular base broad, fleshy (Fig. 2), mandibular articulations displaced medially, not visible externally on head capsule. Distal part of mandible slen-

der and heavily sclerotized, arising medially from base, partly covered by labrum anteriorly and maxilla posteriorly (Fig. 2), terminating in three distinct cuticular teeth visible ventrally (Fig. 4). Maxilla undifferentiated, transversely elongate fleshy lobe, anteriorly abutting labrum; maxillary palp not developed, three trichoid setae situated in middle of maxillary lobe (Fig. 5). Labium narrow anteriorly, broadening posteriorly (Fig. 6), weakly delimited from maxilla by shallow oblique sulcus, retracted relative to maxillae. Salivarial orifice transverse slit surrounded by sclerotized cuticle (barely discernible in early instar larva), situated subapically on labium. Labial palp not developed, paired short trichoid sensilla present posterolaterally.

**Thorax.**—Laterocervicalia absent. Anterior thoracic spiracle well developed, apparently situated slightly anterior to boundary between pro- and mesothorax. Posterior thoracic spiracle vestigial, represented by small, elongate sclerotisation just posterior to meso/metathoracic boundary. Thoracic legs entirely absent.

**Abdomen.**—Ten segments present. Segments 1–8 with well developed spiracles situated laterodorsally (Fig. 7); spiracles circular, rim well sclerotized. Abdominal legs, suranal process, suranal hook, and subanal appendages absent. Anal slit situated posteriorly on segment 10, transversely elongate (Figs 9, 10), shallow (cannot be pried open with a fine needle).

**Hindgut.**—Posterior part of midgut of early instar larva with convoluted walls. Gut contents amorphous, with dark grains. Malpighian tubules not observed. Mid- and hindgut continuous (Fig. 11). Hindgut lined with unsclerotized cuticle becoming progressively thicker posteriorly. Anterior part of hindgut with somewhat thickened epidermis. Hindgut with walls straight, except for 10–12 narrow transverse cuticular folds posteriorly (Figs 11, 12); cuticular folds correspond to concavities in opposite wall. Most of hindgut

surrounded by muscular sheath, except for part posteriorly of cuticular folds (Fig. 12); sheath with transverse and outer longitudinal fibers. Prepupa similar to early instar except for following: Midgut with straight walls, apparently empty except for peritrophic membrane. Boundary between mid- and hindgut marked by one pair of malpighian tubules opening into lateral part of gut. Epidermis retracted from cuticle in posteriormost abdominal segment (Fig. 13), interspace between epidermis and cuticle occupied by amorphous material traversed by elongate tissue strands. Epidermis of anterior part of hindgut not thickened. Muscle sheath not extending very far along hindgut, not reaching region of cuticular folds, comparatively less developed than in early instar larva. Hindgut walls with 18–20 closely appressed cuticular folds (Fig. 14); folds transversely oriented medially, obliquely posteromedially oriented laterally.

## DISCUSSION

The larva of *O. abietinus* closely resembles *O. occidentalis* (see Rohwer and Cushman 1917) in all external features; this is hardly surprising, since the two species are probably sister taxa (Vilhelmsen in press). The more distantly related *G. schauiuslandi* does not differ significantly from *Orussus* spp. in the features that could be observed. However, all three species are comparatively derived within Orussidae, making inferences about the ground plan states for the family tenuous.

The larval head anatomy of Orussidae is highly reduced compared with other non-apocritan Hymenoptera. The eye is entirely absent (a condition also observed in 'siricoid' superfamilies), the antenna is one-segmented and of the mouthparts, only the mandibles appear to be functional, both the maxilla and labium having lost all traces of endites and palps and being immovable relative to the head capsule. In contrast, most 'Symphyta' have multi-segmented antenna as well as dif-

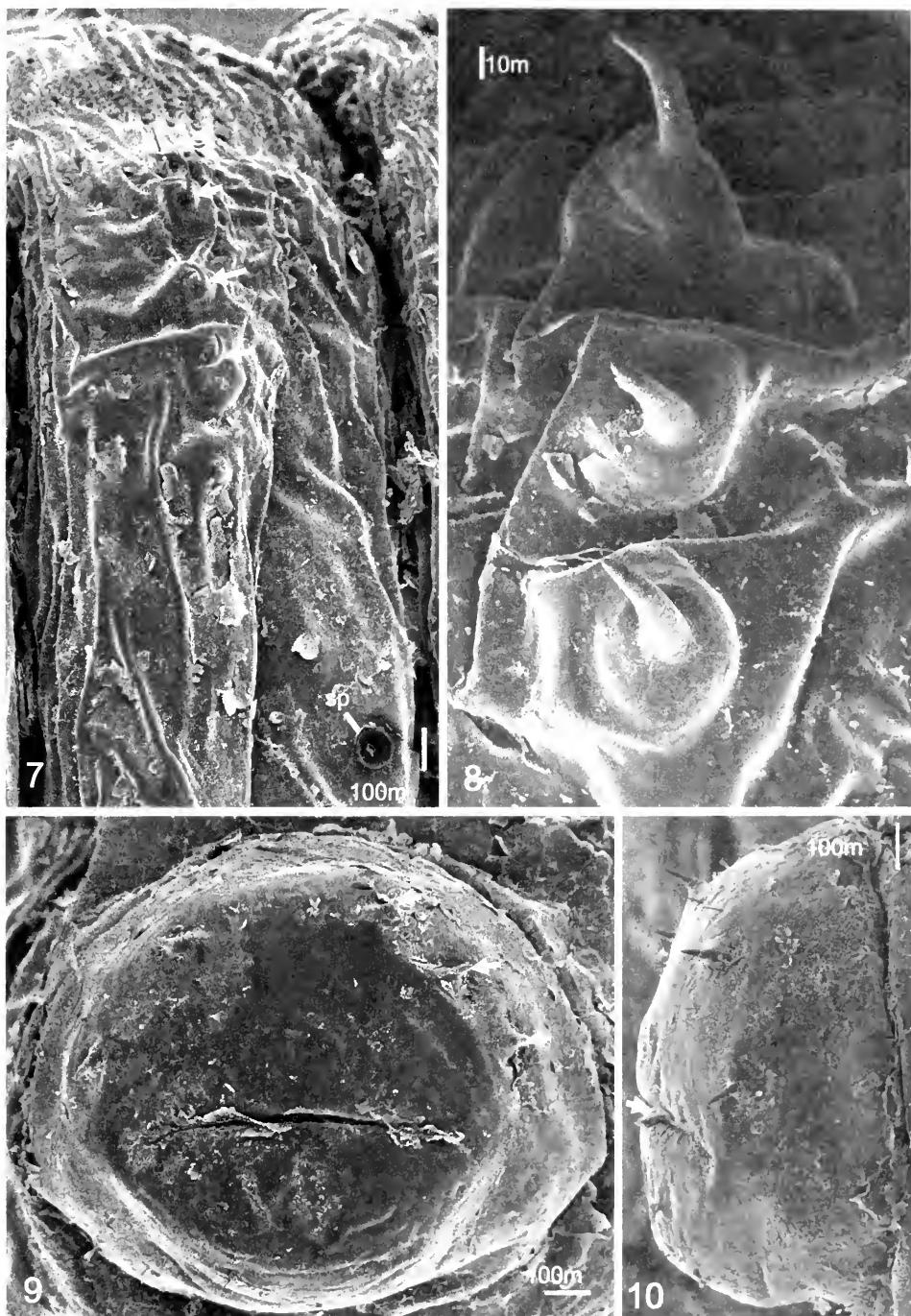
ferentiated endites and palps on the maxilla and labium (see Yuasa 1922). The mandibles of herbivorous 'Symphyta' are usually well sclerotized throughout with external articulations and broad shearing teeth distally. The condition of the mandibles (partly concealed by labrum and maxilla, proximal part unsclerotized, distal part narrowed, see also Rohwer and Cushman 1917, fig. 2a) observed in Orussidae is apparently similar to that of *Schlettererius cinctipes* (Cresson) (Stephanidae; Short 1978, fig. 20; Taylor 1967). Generally, the head anatomy of orussid larva is much closer to that of Apocrita than of other 'Symphyta'. With regard to maxillar and labial palps, those of Orussidae are even more reduced than some Apocrita (e.g., some Ichneumonoidea (Finlayson 1987) and Aculeata (Evans 1987; McGinley 1987)), which have papilliform, one-segmented palps.

The thoracic and abdominal anatomy of the larvae of Orussidae and Apocrita are also reduced relative to more basal Hymenoptera. The laterocervicalia, which in representatives of most 'symphytan' superfamilies articulates with the head capsule anteriorly and connects to the pronotum posteriorly (Vilhelmsen unpubl.), is entirely absent in Orussidae (see also Parker 1935) and apparently also in Apocrita, providing a closer integration of the head and thorax in the two latter taxa. The thoracic legs are entirely absent, having become progressively reduced within the basal lineages of the Hymenoptera (Vilhelmsen 2001). A suranal process, a heavily sclerotized projection on the 10th abdominal segment dorsally of the anal slit prominent in Cephidae, Anaxyelidae, Siricidae, and Xiphydriidae (see Yuasa 1922, pl. xii) is absent from Orussidae and Apocrita. The transverse rows of cuticular spines dorsally have been reported only from *Schlettererius cinctipes* (Stephanidae; Taylor 1967) outside the Orussidae, although in this species, they are only present in the prepupa. Their function in

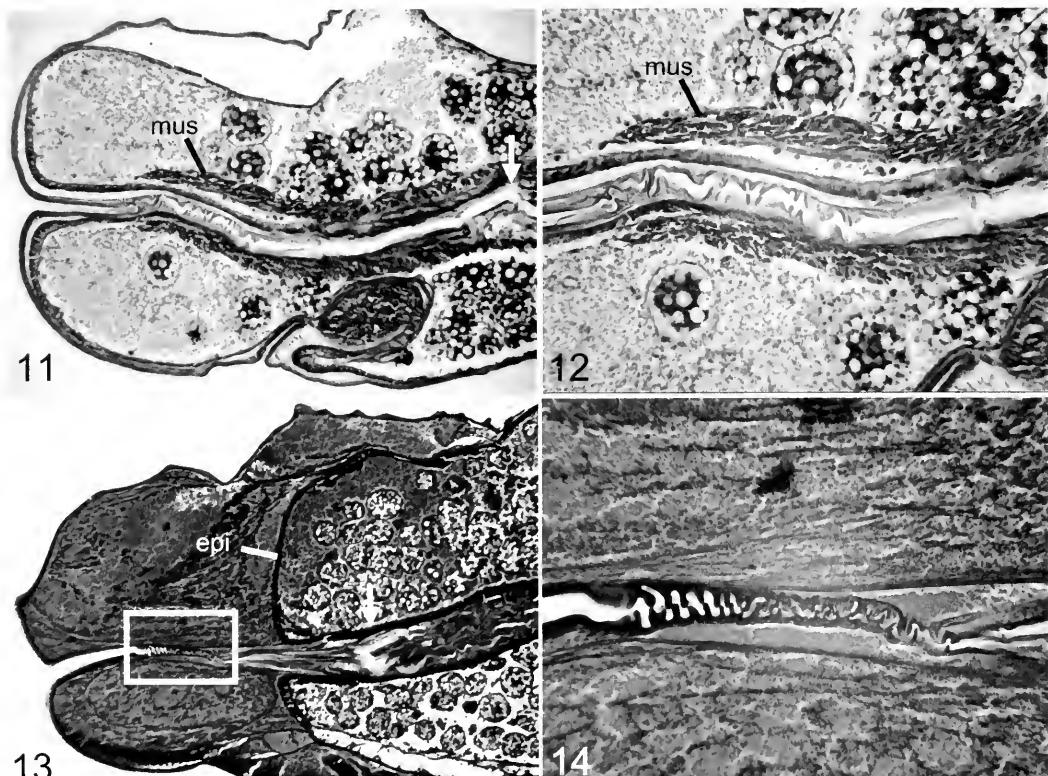
orussid larvae is perhaps to facilitate movement along wood galleries, increased leverage being provided by the deep dorsal furrows between the body segments. Cooper (1953) observed oviposition by female *Orussus* in wood galleries some distance from potential hosts; he interpreted this as indicating that the larvae might be frass feeders. Alternatively, the early instar larva might actively seek out the host within its galleries, if the female was unable to reach the host with its ovipositor; this possibility was considered but rejected by Cooper.

Given the well corroborated monophyly of Orussidae + Apocrita, the interpretation of the phylogenetic significance of the shared reductional features in the larval anatomy is fairly straightforward: they represent synapomorphies for these two taxa. Some of these characters have already been included in recent phylogenetic treatments of the Hymenoptera (e.g., number of larval antennal segments, reduction of larval thoracic legs, characters 224 and 228 in Vilhelmsen 2001), whereas as others (reduced maxillar and labial appendages, absence of laterocervicalia) have been ignored until now.

The functional significance of the anatomical modifications can be interpreted in the context of the shift in larval lifestyle from herbivorous/woodboring to carnivorous/parasitoid having taken place in the common ancestor of Orussidae and Apocrita. The reduced sensory capabilities (loss of eyes, reduction of antennae) reflect the confined habitat (galleries in wood) of the larvae of the earliest parasitoid wasps and their closest relatives, the woodwasps. The reduction of the mouthparts is perhaps a consequence of the shift in food source from particulate plant matter that requires considerable handling and chewing to a much less demanding diet of insect body fluids. Once an ectoparasitoid wasp larva is in contact with its host, it is required to do little more than puncture the integument of the latter to gain access



Figs. 7-10. *Orussus abietinus*, abdominal anatomy. 7-8, Early instar larva, posterior to the left. 7, Dorsal part of abdominal segment; arrows indicate cuticular spines; sp = spiracle. 8, Recurved cuticular spines. 9-10, Prepupa. 9, 10th abdominal segment, posterior view; arrows indicate cuticular spines. 10, Same, lateral view. arrow indicates anal slit.



Figs. 11–14. *1* *Orussus abietinus*, internal anatomy of hindgut (posterior to left). 11–12. Early instar larva. 11, Overview of hindgut region, arrow indicates transition between mid- and hindgut: mus = muscle sheath. 12, Details of cuticular folds in hindgut. 13–14, Prepupa. 13, Overview of hindgut region, arrow indicates transition between mid- and hindgut, rectangle indicates approximate extent of Fig. 14: epi = retracted epidermis. 14, Details of cuticular folds in hindgut.

to its contents, a purpose for which the narrow, pointed mandibles of the orussid larva probably is admirably suited. The reduction of the locomotory apparatus again reflects the confined larval habitat, being taken even further than in the Cephidae and woodwasp families, which retain vestiges of thoracic legs. The suranal process present in these taxa is also absent in Orussidae and Apocrita, a change that perhaps is correlated with the shift in food source. This feature is needed as a brace by the endophytophagous taxa when chewing a tunnel through tough plant material; the larvae of Orussidae and wood-living Apocrita do not chew their own tunnels and hence do not need a posterior brace.

The configuration of the hindgut in the early instar larva and prepupa of *Orussus* is unlike anything else reported from Hymenoptera. The cuticular folds matching concavities in the opposite walls and the extension of the muscular sheath surrounding the hindgut to include the part with the folds indicate that even though the mid- and hindgut are not anatomically separated, the larva is able to close the hindgut by muscular action. In the prepupa, the opposite walls of the hindgut abut in the region with the cuticular folds even though the muscular sheath does not extend this far back; this may be caused by the loosening of the prepupal cuticle and the retraction of the epidermis and associated musculature prior to pupation.

The connection between mid- and hindgut in 'Symphyta' whose embryology have been examined (e.g., *Pontania caprae* Linnaeus (Tenthredinidae), see Ivanova-Kasas 1959) is established already at the time of hatching from the egg. The anatomical separation caused by the failure of the two gut sections to join during the embryological development (Hanson and Gauld 1995) has been reported from a wide range of apocritan superfamilies: Ceraphronoidea (Megaspilidae: *Dendrocerus* (= *Lygocerus*) spp., see Haviland 1920a, fig. 14), Chalcidoidea (Pteromalidae: *Spaolangia muscidarum* Richardson, see Richardson 1922, fig. 7; *Asaphes vulgaris* Walker, *Pachycrepis clavata* Walker, see Haviland 1922), Cynipoidea (Figitidae: *Charips* spp., see Haviland 1920b, fig. 11a), Ichneumonoidea (Ichneumonidae: *Pimpla turionellae* (Linnaeus), see Führer and Willers 1986, fig. 3), Platygastroidea (Platygastriidae spp., see Marchal 1906, pl. xviii: 24), Proctotrupoidea (Proctotrupidae: *Phaenoserphus viator* (Haliday), see Eastham 1929, fig. 12). It is often accompanied by considerable differentiation between hindgut regions (epidermis and muscle layer of variable thickness, formation of valves; e.g., Eastham 1929, Führer and Willers 1986, Haviland 1920b) that is less conspicuous in *O. abietinus*. However, many 'Symphyta' also have the hindgut differentiated into several regions (Maxwell 1955).

The functional and phylogenetic significance of the larval hindgut anatomy of *Orussus* is difficult to interpret without further information about the orussid lifestyle and investigation of larvae of some of the basalmost apocritan ectoparasitoid taxa (e.g., Stephanidae and Megalyridae). It is possible, but entirely conjectural, that the cuticular folds help the orussid larva to clamp its hindgut shut for most of its development, thus preventing contamination of its host. However, the expulsion of a meconium prior to pupation as seen in most apocritans examined was not observed in a couple of hatchings of *O. abie-*

*tinus* (Vilhelmsen unpubl.). The anatomical position (posteriorly in the hindgut) of the cuticular folds in *Orussus* is not homologous with the position (boundary between mid- and hindgut) of the separation of the gut sections in Apocrita, making it unlikely that the latter evolved from the former. Thus, this study has revealed another intriguing feature occurring in parasitic Hymenoptera, rather than elucidating the evolution of an already known trait.

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## NOTE

### First Report of Male Sleeping Aggregations in the Pollen Wasp *Celonites abbreviatus* (Villers, 1789) (Hymenoptera: Vespidae: Masarinae)

F. AMIET AND V. MAUSS

(FA) Forstrstr. 7, CH-4500 Solothurn, Switzerland;  
(VM) Staatliches Museum für Naturkunde, Abt. Entomologie, Rosenstein 1,  
D-70191 Stuttgart, Germany, email: volker.mauss@stechimmenschutz.de

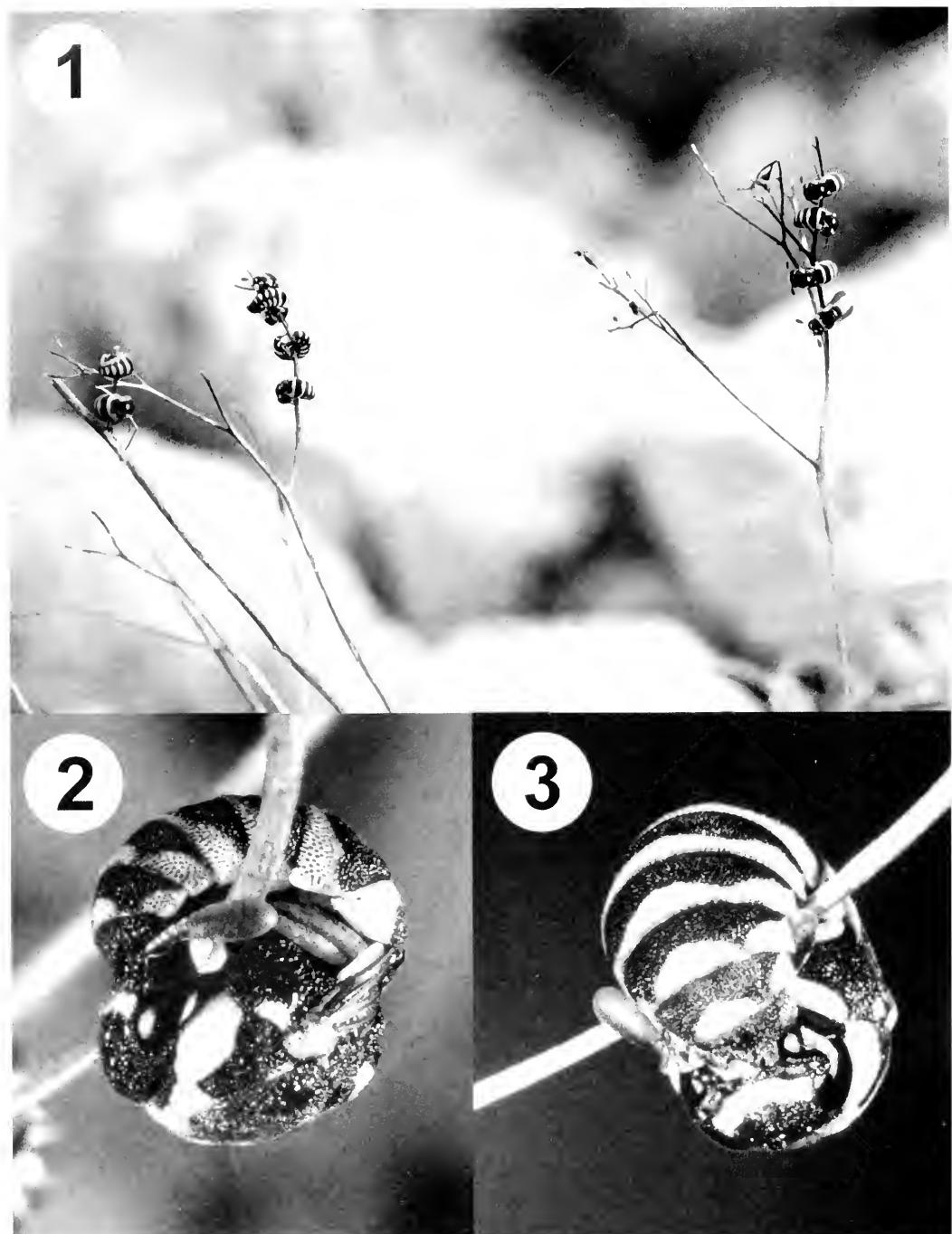
The nightly resting behaviour of solitary and social bees, and probably also of many other Aculeata, constitutes a sleep-like state with many neurophysiological parallels to mammalian sleep (Kaiser and Steiner-Kaiser 1983, Kaiser 1988, 1995). Sleeping behaviour has been well documented in many species of solitary wasps (O'Neill 2001: 294). Interspecific variation of sleep is evident in (1) the location of the sleeping site, (2) the postures adopted during sleep, and (3) whether the wasp sleeps in the company of other members of its own species, members of the opposite sex, and members of other species (O'Neill 2001: 294). In contrast, present knowledge of sleeping behaviour of male pollen wasps is poor. Males of some species of the genus *Ceramius* seek overnight shelter in conspecific nests that may or may not contain females (Brauns 1910, Gess 1996: 63, Mauss 1996). *Celonites andrei* Brauns was observed to spend the night sleeping on vegetation (Brauns 1910), and a male of *Celonites abbreviatus* slept curled up around a blade of grass (Bischoff 1927: Fig. 29). Males of *Masarina mixta* Richards were commonly observed to sleep in bell-shaped flowers of *Wahlenbergia* (Campanulaceae) on which they and the females forage during the daytime (Gess 1996: 63).

Male sleeping aggregations have not previously been recorded for any species of the Masarinae (Gess 1996: 63), although

they have been observed for numerous other wasps and bees (summarised by Bischoff 1927: 62–64, Westrich 1989: 124, O'Neill 2001, Wcislo 2003). We describe here for the first time, male sleeping aggregations in *C. abbreviatus* which were discovered at two different locations in Switzerland.

(1) Pfynwald (07°35'E 46°38'N), Rhone Valley, Wallis, Switzerland, July 1977, obs. F. Amiet, A. Krebs: In the evening four males were sleeping in an aggregation on a withered, branched stem of an herbaceous perennial plant about 0.2 m above the ground. A photograph of this aggregation was reproduced in Witt (1998: 192 bottom right), however it was not further commented on, and it was erroneously shown in the vertical position. Distance between the males varied from 0 (i.e., in physical contact with each other) to about 8 mm. All males adopted the same typical posture: They curled their bodies around the stem so that the tip of their metasoma covered the ventral part of the clypeus. Antennae and legs were pulled up under the mesosoma, and the wings were folded underneath the metasoma (Figs. 2, 3, the identical posture as in Bischoff 1927, fig. 29). The males were observed to aggregate and sleep on the same stem on several consecutive nights.

(2) Berner Oberland near Boltigen (07°22'E 46°38'N), Simmental, Switzer-



Figs. 1-3. *Celonites abbreviatus*, male sleeping aggregation. 1, Berner Oberland, August 1997 (actual body length of males about 8 mm). 2, Sleeping posture (viewed from left), Pfynwald, July 1977 (Photo: A. Krebs). 3, Sleeping posture (viewed from ventral), Pfynwald, July 1977.

land, at the foot of a scree slope, August 1997, obs. F. Amiet: The sky was cloudy and whenever the sun became obscured by a larger cloud some males of *C. abbreviatus* alighted on two withered stems of herbaceous perennial plants about 0.25 m above the ground (Fig. 1) and adopted the typical sleeping posture. Moments later when the sun emerged again some of these males became active and flew away. From three o'clock p.m. (Central European Time) onward all the males remained in the sleeping posture on the stems although the sun still shined intermittently. At four o'clock p.m. it commenced to rain. A maximum of 14 males were observed on both stems. Distance between the sleeping males in the aggregation ranged from 0 to about 8 mm.

Other clades of the Vespidae in which male sleeping aggregations occur are the Euparagiinae (*Euparagia scutellaris* Cresson, Moore 1975) and at least six genera of the Eumeninae (*Labus*, Bischoff 1927: 62, and *Ancistrocerus*, *Eumenes*, *Pterocheilus*, *Rhynchium*, *Stenodynerus*, Linsley 1962). The sleeping postures of the eumenine wasps studied differ distinctly from that in *Celonites abbreviatus*: Males of the Eumeninae attach themselves to the substrate with their legs and mandibles (Linsley 1962). Their wings are folded but extend outward at an angle of approximately 45 degrees. Unfortunately, the sleeping posture of *Euparagia* cannot be brought into context since it was not described in sufficient detail by Moore (1975). The evolutionary significance of aggregated sleeping is uncertain (Evans et al. 1986), but it has been suggested that it offers protection against predators, may influence thermoregulation or may be associated with

mating behaviour (cf. Freeman and Johnston 1978).

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Dr. E. Eric Grissell  
Systematic Entomology Laboratory, USDA  
Smithsonian Institution  
P.O. Box 37012  
National Museum of Natural History CE 520, MRC168  
Washington, DC 20013-7012  
Phone: (202) 382-1781 Fax: (202) 786-9422 E-mail: egrissel@sel.barc.usda.gov



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